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SOIL PROPERTIES DETERMINING THE BOTANICAL COMPOSITION OF PASTURES IN WEST VIRGINIA [1]

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INTRODUCTION

Numerous trials have shown that with proper fertilizer and lime treatments, Kentucky bluegrass and white clover will replace *Danthonia* and other relatively undesirable native grasses in West Virginia pastures. It would be expected, therefore, that some correlation should exist between the botanical composition of a pasture and the fertility and reaction of the soil as measured by laboratory methods. Although the incidence of certain plant species in relation to soil reaction has been extensively studied in Europe and to a lesser extent in the United States (*8, 11, 16, 20, 23*) [3] relatively little attention has been given to agricultural plants and even less to pasture species. Moreover, most of the work was done prior to the development of suitable methods for the determination of the fertility level of the soil, and consequently little consideration was given to soil factors other than pH values. The problem of plant distribution, however, appears too complex to be explained by any one factor.

Cooper (*7*) determined the pH of 2,317 soil samples from 546 pastures in New York and recorded the dominant species growing at the different pH values. He concluded that soil reaction alone was not an important factor in determining the distribution of pasture species, and suggested that a well-balanced supply of available cations and anions having a relatively high oxidation-reduction potential is much more effective than the pH value of the soil in determining the dominance of various pasture species.

Dix (*9*) determined pH value, total phosphorus, acid-soluble calcium and potassium, total nitrogen, loss on ignition, and mechanical analysis of 53 pasture soils in Germany. He found no satisfactory agreement between the pasture flora and any of the soil properties studied, and concluded that all the soils were sufficiently productive to support the better types of plants. It is generally recognized, however, that neither total phosphorus nor acid-soluble calcium or potassium is a satisfactory measure of the availability of these elements to the plants.

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[2] The writer wishes to express his sincere appreciation for the many helpful suggestions and criticisms offered by Dr. W. H. Pierre, under whose supervision this work was done; and to Dr. R. J. Garber for helpful suggestions in connection with the interpretation of the statistical studies.

[3] Reference is made by number (italic) to Literature Cited, p. 896.

The objectives of the present investigation were as follows: (1) To determine the reaction of fertility of some of the important pasture soils of the State as measured by laboratory methods; (2) to determine the relationship between these properties and the botanical composition of the pasture; and (3) to determine the minimum fertility and reaction levels necessary to maintain a stand of Kentucky bluegrass (*Poa pratensis* L.) and white clover (*Trifolium repens* L.).

EXPERIMENTAL PROCEDURE AND METHODS

FIELD PROCEDURE

In the fall of 1934, samples of the 0- to 3- and 3- to 6-inch soil layers[4] were taken from 126 areas in 43 pastures, avoiding pastures that had been reseeded or that had received lime, fertilizer, or manure during the preceding 5 or 6 years. Pastures that were lightly grazed were also avoided except in a few cases, which will be discussed later. The soil samples were air-dried, screened, placed in ice-cream containers, and kept in a well-ventilated room in the basement of the laboratory.

Botanical estimates, giving the percentage of the total area occupied by weeds and each of the pasture grasses and legumes, were made at the time the soil samples were taken and again in early August 1935, except in a few cases where the areas had been plowed or otherwise disturbed in the meantime. The data for each area included also a description of the soil type, depth of surface soil, percentage slope, direction of slope, intensity of grazing, and any miscellaneous observations.

Although samples were taken from nine soil series, most of the studies were conducted either on Hagerstown silty clay loam in the vicinity of Martinsburg, or on Dekalb silt loam in the vicinity of Morgantown. The Hagerstown soils are of limestone origin and are among the most productive upland soils in the State. The Dekalb soils, on the other hand, are derived from noncalcareous shales and sandstones and are among the least productive of the upland soils, yet will produce very good crops if limed, fertilized, and properly managed.

CHEMICAL STUDIES

The soil samples representing the 0- to 3-inch layer were analyzed for pH, available phosphate, total nitrogen, total exchange capacity, total exchangeable bases, exchangeable potassium, and in a few cases, exchangeable calcium, magnesium, and sodium. The samples from the 3- to 6-inch layer were analyzed for pH, available phosphate, and in certain of the Dekalb samples, total nitrogen.

The pH values were determined potentiometrically on a 1 to 2½ soil-water suspension, using a glass electrode. Available phosphate was determined by Truog's (*21*) well-known laboratory method and expressed as parts per million of dry soil. Total nitrogen was determined by the standard Gunning-Hibbard method.

Since total exchange capacity, total exchangeable bases, and exchangeable calcium, magnesium, and potassium were all determined on the same sample, the soil was first leached with distilled water in order to remove soluble calcium, magnesium, and potassium. Total exchange capacity was then determined by the method of Conrey and

[4] Sampling to a depth of 3 inches for pasture studies is in accordance with the recommendations of Askew et al. (*1*).

Schollenberger (*6*). Total exchangeable bases were determined by the method of Bray and Wilhite (*4*), except that only an aliquot of the solution was titrated. Other aliquots of this solution were used for the determination of calcium, magnesium, and potassium. Calcium was precipitated as the oxalate, the precipitate collected by centrifuging, and calcium then determined by titrating with standard potassium permanganate. The supernatant liquid and wash solution from the calcium determination were used for the determination of magnesium (any iron or aluminum present was first removed by precipitation as the phosphate). Magnesium was precipitated by the method of Kramer and Tisdall (*15*), except that the precipitate of magnesium ammonium phosphate was collected by centrifuging rather than by filtering. The phosphorus content of the precipitate was determined by the method of Fiske and Subbarow (*13*), and the magnesium content calculated from the amount of phosphorus present. Potassium was determined essentially by the cobaltinitrite method as outlined by Van Rysselberge (*22*), except that the precipitate was collected by centrifuging rather than by filtering.

Exchangeable sodium was obtained by the method of Salgado (*19*), and the sodium content of the solution was determined by the method of Barber and Kolthoff (*2*), which was found by Bray (*3*) to give satisfactory results when applied to replaceable sodium in soils.

EXPERIMENTAL DATA

BOTANICAL COMPOSITION

Although bunch grasses such as *Danthonia* maintain a reasonably uniform percentage ground cover during the season, a sod of Kentucky bluegrass and white clover becomes relatively thin during the hot, dry summer months. The difference between the estimates for 1934 and 1935 of the percentage bare space, Kentucky bluegrass, and white clover on the Hagerstown soils (table 1) emphasizes the importance of considering seasonal factors. In 1934 the botanical estimates were made early in December, when soil moisture was not a limiting factor, and when Kentucky bluegrass was still in a thrifty condition. The 1935 estimates, on the other hand, were made early in August after a severe drought, so that soil moisture was an important limiting factor. Consequently the proportion of bare space was higher, and that of Kentucky bluegrass lower, in 1935 than in 1934. Thus in the areas consisting of at least 10 percent of Kentucky bluegrass plus white clover in 1934, the average values for the sum of these species were 58 and 33, respectively, for 1934 and 1935.

The index of correlation[5], however, between these values for 1934 and 1935 is 0.928. This means that the square of 0.928 or 86 percent of the variations in the values for Kentucky bluegrass plus white clover in 1935 can be explained by similar variations in the values for 1934. Since the value of n in this case is 20, the probable minimum correlation is 0.85. This means that the chances are 19 to 1 that the true correlation existing in the universe from which the sample was drawn is at least 0.85.

[5] The statistical methods were those described by Ezekiel (*12*).

TABLE 1.—*Estimated percentages of bare space, Kentucky bluegrass, and white clover on the Hagerstown soil areas in December 1934 and in August 1935*

Sample no.	Pasture no.	Bare space		Kentucky bluegrass		White clover	
		1934	1935	1934	1935	1934	1935
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
101	30	8	35	80	55	2	0
102	30	12	35	48	40	15	2
103	31	15	35	75	62	0	0
104	31	25	65	50	20	0	0
105	31	15	[1] 81	0	2	3	1
106	32	8	35	70	57	10	3
107	32	5	50	68	30	15	6
108	33	5	35	70	55	15	3
109	34	20	57	55	25	10	3
110	34	15	[1] 61	30	15	0	0
111	34	13	35	7	5	5	1
112	34	15	35	71	51	4	1
113	35	73	75	2	0	0	0
114	35	45	62	35	3	0	0
115	36	25	62	28	5	0	0
116	36	12	25	63	60	10	1
117	37	15	36	2	0	0	0
118	38	25	[1] 70	1	0	0	0
119	38	15	52	50	20	0	2
120	39	30	50	35	12	2	0
121	39	20	52	2	0	0	0
122	40	10	40	71	50	15	5
123	41	20	38	49	15	1	3
124	41	20	[1] 45	5	0	0	1
125	42	15	48	62	40	3	2
126	43	20	54	40	15	0	1
Average		19	49	41	24	4	1

[1] Predominantly annual grasses in 1934.

In the other soils (samples 1–100), the difference between the moisture content of the soil prior to the two botanical estimates was not so great as in the Hagerstown soils. The average values for the sum of Kentucky bluegrass and white clover, in the samples consisting of at least 10 percent of these species in 1934, were 52 and 38, respectively, for 1934 and 1935. The index of correlation between the values for these 2 years is 0.919 (n is 43, and the probable minimum correlation is 0.87).

All subsequent references to botanical estimates will mean those made in 1934, since these were affected less by lack of soil moisture than those made in 1935.

The percentage of bare space, Kentucky bluegrass, white clover, and *Danthonia* on those areas discussed later in connection with figures 4 to 8 are given in table 2. (The species not shown in the table consist largely of weeds, bentgrasses, and native grasses.) These areas are somewhat better than the average, however, because samples were excluded if more than one chemical property was found to be limiting.

TABLE 2.—*Chemical properties of soils and botanical composition of corresponding pastures*

Sample no.	Pasture no.	Soil type	pH	Base saturation	Exchangeable bases	PO_4	N	K	Bare space	Kentucky bluegrass	White clover	Danthonia spicata
				Pct.	*Milli-equiva-lents*	*P p. m.*	*Pct.*	*Milli-equiva-lents*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
1	1	Upshur silty clay loam	5.65	54	9.70	18.0	0.340	0.80	15	45	6	2
10	4	Westmoreland silt loam	5.90	72	14.90	24.0	.368	.27	15	70	3	0
13	5	Dekalb sandy loam	5.54	53	5.80	33.5	.274	.21	40	50	0	0
19	6	Elk silt loam	4.95	38	3.68	20.5	.211	.18	25	0	0	65
21	7	Dekalb silt loam	5.24	33	6.20	20.0	.464	.45	25	4	0	57
24	8	Dekalb fine sandy loam	5.40	50	5.81	36.0	.362	.27	25	50	0	0
26	8	do	5.02	23	2.91	32.0	.376	.19	30	2	0	53
27	9	Dekalb silt loam	5.86	71	15.25	27.0	.474	1.00	8	56	3	0
31	10	do	4.84	16	2.33	18.5	.333	.29	15	0	0	75
34	13	Dekalb silty clay loam	5.46	58	9.57	19.0	.288	.21	12	75	4	0
37	14	Elk silt loam	4.96	31	3.02	33.0	.217	.32	20	44	0	0
44	18	Dekalb silt loam	5.21	49	8.42	18.0	.383	.35	20	42	2	1
45	19	do	5.06	30	4.91	21.5	.330	.24	15	4	2	1
50	20	Elk silt loam	4.81	27	2.23	29.5	.187	.20	50	5	0	17
53	21	Dekalb silt loam	5.31	63	11.57	24.0	.384	.41	10	76	2	0
55	21	do	5.59	75	21.00	18.5	.582	.85	8	71	0	0
59	23	do	5.28	50	9.34	24.0	.331	.34	15	65	0	0
60	23	do	5.22	49	9.76	24.5	.345	.21	30	27	3	0
61	23	do	5.13	41	7.52	35.0	.328	.45	20	5	5	0
62	23	do	4.74	21	3.11	19.5	.264	.32	5	0	0	78
64	24	Dekalb silty clay loam	5.50	78	13.91	20.0	.274	.46	15	80	0	2
73	2	Dekalb silt loam	6.32	82	8.81	23.5	.242	1.64	5	80	2	0
78	25	do	5.22	52	8.27	23.0	.367	.53	5	70	3	0
79	25	do	4.99	33	5.46	15.0	.356	.41	10	60	0	10
81	25	do	4.97	37	5.91	25.0	.349	.33	50	29	0	1
89	27	Upshur silty clay loam	5.05	44	8.30	25.0	.472	.36	5	85	8	0
93	28	Westmoreland silt loam	4.83	26	3.27	18.5	.282	.18	15	62	0	0
96	28	do	5.47	51	7.29	30.0	.277	.25	12	68	0	0
97	29	Pope silt loam	5.75	78	15.98	35.0	.312	.22	12	80	3	0
102	30	Hagerstown silty clay loam	6.46	91	12.96	24.5	.240	.45	12	48	15	0
103	31	do	6.03	75	6.47	18.0	.156	.51	15	75	0	0
106	32	do	5.99	77	7.47	20.0	.210	.40	8	70	10	0
107	32	do	6.28	85	10.17	42.0	.214	.24	5	68	15	0
108	33	do	5.68	63	5.27	18.5	.193	.32	5	70	15	0
109	34	do	6.82	97	10.68	14.0	.201	.21	20	55	10	0
110	34	do	6.16	78	6.10	8.0	.149	.35	15	30	0	0
112	34	do	6.87	100	16.50	35.0	.258	.46	15	71	4	0
113	35	do	6.55	94	14.84	8.5	.155	.42	73	2	0	0
114	35	do	6.03	88	9.85	10.5	.147	.35	45	35	0	0
115	36	do	6.31	91	9.90	13.5	.192	.40	25	28	0	2
116	36	do	7.44	100	27.70	40.0	.383	1.18	12	63	10	0
118	38	do	5.81	69	5.74	7.0	.146	.24	25	1	0	0
119	38	do	5.96	68	5.55	11.0	.147	.27	15	50	0	0
120	39	do	6.87	85	10.60	12.5	.177	.24	30	35	2	0
125	42	do	6.47	87	8.71	18.0	.193	.23	15	62	3	0
126	43	do	6.31	83	7.99	12.0	.159	.26	20	40	0	0

CHEMICAL PROPERTIES OF THE SOILS

The more important laboratory data on the 0- to 3-inch soil layer of those samples discussed later in connection with figures 4 to 8 are summarized in table 2. A study of all samples, however, shows that the pH values of the majority of the Hagerstown soils vary from about 5.9 to 6.9, whereas in the Dekalb and other soils the range is in most cases between 4.8 and 5.6. The total nitrogen averages 0.303 percent for the Dekalb soils and 0.185 for the Hagerstown. This difference in nitrogen content is believed to be due largely to the fact that the Hagerstown soils have been cropped more recently; for Bryan and Deatrick (*5*), in their study of fields largely in a regular rotation, found no difference between the nitrogen content of Hagerstown and Dekalb soils.

TABLE 3.—*pH values, available phosphate, and nitrogen of the 0- to 3- and 3- to 6-inch layers of Dekalb soils that have been in permanent pasture about 20 to 50 years*

Sample no.	Depth of surface soil	Kentucky bluegrass plus white clover	pH of—		PO_4 in—		N in—	
			0- to 3-inch layer	3- to 6-inch layer	0- to 3-inch layer	3- to 6-inch layer	0- to 3-inch layer	3- to 6-inch layer
	Inches	*Percent*			*P. p. m.*	*P. p. m.*	*Percent*	*Percent*
38	4–5	63	5.32	5.64	13.0	5.5	0.270	0.096
39	4–5	2	5.29	5.52	11.0	5.0	.245	.113
21	5	4	5.24	5.15	20.0	10.0	.464	.316
26	5	2	5.02	4.95	32.0	25.0	.376	.248
75	5	5	5.31	5.48	9.0	<5.0	.192	.088
6	5–6	3	5.07	5.60	9.5	<5.0	.267	.146
Average	4–6	13			15.7	<9.2	.302	.168
4	6	66	5.50	5.59	16.0	5.5	.330	.170
13	6	50	5.54	5.59	33.5	26.5	.274	.233
16	6	55	5.23	4.99	16.0	7.0	.214	.139
17	6	1	4.89	4.94	10.5	8.5	.157	.115
29	6	1	4.88	5.14	17.0	8.5	.290	.165
33	6	5	5.20	5.28	6.5	<5.0	.205	.158
34	6	79	5.46	5.39	19.0	9.5	.288	.155
44	6	44	5.21	5.47	18.0	17.5	.383	.207
48	6	2	4.75	5.08	15.0	9.5	.256	.134
70	6	40	5.10	5.25	9.0	5.0	.231	.155
71	6	15	4.89	5.01	10.5	5.0	.223	.166
77	6	5	4.86	4.98	14.0	8.5	.356	.174
78	6	73	5.22	5.03	23.0	8.5	.367	.166
Average	6	34			16.0	<9.6	.275	.164
45	7	6	5.06	5.41	21.5	23.0	.330	.230
46	7	3	5.20	5.59	9.5	6.5	.314	.202
67	7	67	5.45	5.69	10.0	5.5	.254	.159
79	7–8	60	4.99	4.96	15.0	5.0	.356	.163
73	8	82	6.32	6.25	23.5	11.0	.242	.132
55	9	71	5.59	5.76	18.5	5.5	.582	.330
59	9	65	5.28	5.39	24.0	7.5	.331	.256
60	9	30	5.22	5.42	24.5	9.5	.345	.276
61	9	10	5.13	5.03	35.0	13.5	.328	.250
27	9–10	59	5.86	5.86	27.0	12.5	.474	.302
53	12	78	5.31	5.31	24.0	8.5	.384	.183
Average	7–12	48			21.1	9.8	.358	.226
Grand average	4–12	35			17.8	<9.6	.311	.188

COMPARISON OF THE 0- TO 3- AND 3- TO 6-INCH SOIL LAYERS

Table 3 gives the pH values, available phosphate, and percentage nitrogen of the 0- to 3- and 3- to 6-inch layers of Dekalb soils that have been in permanent pasture for about 20 to 50 years but have received no lime or fertilizer. The 0- to 3-inch layer averages 65 percent higher in total nitrogen, 85 percent higher in available phosphate, and slightly lower in pH than the 3- to 6-inch layer. Since practically all West Virginia pastures were formerly tilled fields, the difference between the nitrogen content of the 0- to 3-inch and the 3- to 6-inch layers presumably is a rough measure of the quantity of nitrogen that has accumulated during the period in which the area has been in pasture. On the basis of this assumption there has been an average total increase of approximately 1,000 pounds per acre of nitrogen. This increase is too great to be explained by the use of supplementary feed while the cattle are on pasture. Moreover, it cannot be attributed to surface washing from higher areas, for most of the samples were taken either from the tops of hills or from areas where the chance for loss from erosion was as great as the chance for accumulation by deposition. It is evident, therefore, that this increase must have been

due partly to fixation by micro-organisms, either symbiotic or non-symbiotic. The difference in available phosphate between the 0- to 3- and the 3- to 6-inch layers is probably due to a combination of several factors. In the first place, the plants obtain a certain amount of phosphorus from below the 3-inch level. A large part of this phosphorus is returned to the soil in the form of animal manure or in uneaten herbage, and undoubtedly most of it is retained in the surface 3 inches. Moreover, the high organic-matter content of the surface layer would tend to decrease the amount of phosphorus fixed in a relatively unavailable form.

All subsequent references to soil properties will mean those of the 0- to 3-inch layer, since these were found to be a better indication of the botanical composition of the pasture than those of the 3- to 6-inch layer.

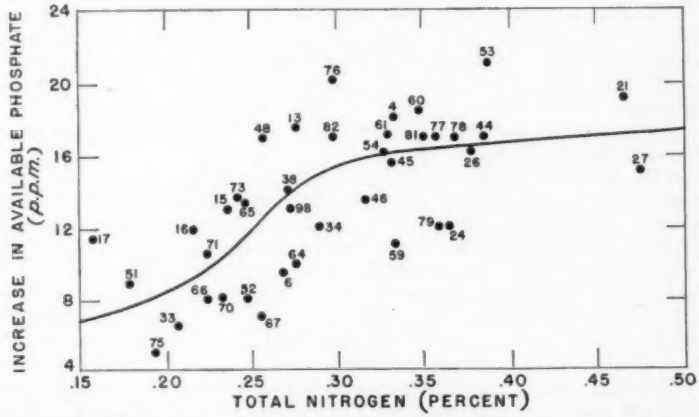

FIGURE 1.—The effect of the nitrogen content of the Dekalb soil on the increase in available phosphate (determined by Truog's method) during storage for 1 year in an air-dry condition. Numbers represent soil-sample numbers.

CHANGES IN AVAILABLE PHOSPHATE CONTENT OF THE SOILS DURING STORAGE

The values for available phosphate that are given in table 2 were obtained within a few weeks after the soil samples were collected. Determinations of available phosphate were repeated on a number of samples about 1 year after the original determinations were made. In the 41 Dekalb soil samples studied there was an average increase of 78 percent or 13.7 parts per million of available phosphate during storage for 1 year.[6] As shown in figure 1, the magnitude of the increase was associated with the organic-matter content of the soils as indicated by the total nitrogen content. This suggests that during the period of storage part of the organic phosphorus was changed to an inorganic form. Organic phosphorus was not determined in these samples, but other factors such as soil reaction, soil texture, and the quantity of available inorganic phosphate in the soil had no apparent effect on this change.

[6] These results are contrary to those reported by Dunnewald (*10*) under Wyoming conditions.

In the 22 Hagerstown soil samples studied there was an average increase of only 40 percent, or 7.3 parts per million, of available phosphate during the storage period. These samples, however, averaged only 0.179 percent nitrogen as compared with 0.301 percent for the Dekalb samples in which this relationship was studied.

Under West Virginia conditions it would be expected that the changes in the available phosphate of permanent pasture soils during storage would be greater than those of tilled soils because of the higher organic-matter content of the former. These changes must be taken into consideration when comparisons are made of the available phosphate content of pasture soils, as well as when determining whether or not a pasture would be expected to give profitable returns from the use of phosphate fertilizers.

Relationship Between Various Chemical Properties of the Soils

A statistical analysis of the samples from the Hagerstown soils, many of which have been limed and manured, shows no correlation between pH and either available phosphate or exchangeable potassium, or between available phosphate and either total nitrogen or exchangeable potassium. There is, however, a slight positive correlation between pH and total nitrogen and between exchangeable potassium and total nitrogen.

In the samples from the Dekalb soils, the index of correlation between available phosphate and total nitrogen is 0.569 (n is 44, and the probable minimum correlation is 0.38). Moreover, there is a slight positive correlation between pH and exchangeable potassium. However, if comparisons are made between samples taken from nearby areas within the same pasture (table 5), thereby eliminating as far as possible such factors as the origin and previous cultural treatment of the soil, there is also a positive relationship between pH and available phosphate and between pH and total nitrogen.

There is a straight-line relationship between total exchange capacity and total nitrogen, the coefficient of correlation for all samples being 0.804 (n is 119, and the probable minimum correlation is 0.74). If only one soil type is considered, namely, the Dekalb silt loam, the correlation is 0.864 (n is 44, and the probable minimum correlation is 0.78). In the Hagerstown silty clay loam samples, which are heavier than Dekalb and much lower in organic matter, the coefficient of correlation between total nitrogen and total exchange capacity is 0.832 (n is 24, and the probable minimum correlation is 0.70). This high correlation emphasizes the importance of the organic exchange complex in pasture soils and is especially significant in view of the range in texture of the different soils.

The work of Pierre and Scarseth (*18*) shows that highly weathered soils have a lower degree of saturation at a given pH value than less weathered soils. In this study, where most of the soils have been weathered to about the same extent, the percentage base saturation is rather closely associated with the soil reaction, the index of correlation between the two properties being 0.922 for the whole group of soils (n is 117, and the probable minimum correlation is 0.90). It is of interest also that the correlation for the entire group of soils is even slightly higher than the correlation within either the Dekalb or the Hagerstown

series. The percentage base saturation at different pH values based on the regression curve is as follows:

Percentage base saturation:	*pH*	Percentage base saturation—Con.	*pH*
20	4. 80	68	5. 60
32	5. 00	75	5. 80
45	5. 20	85	6. 20
57	5. 40	91	6. 50

In spite of the high correlation there is considerable variation in the percentage base saturation of different soils at the same pH value. However, it is recognized that all soils do not have the same ratio of

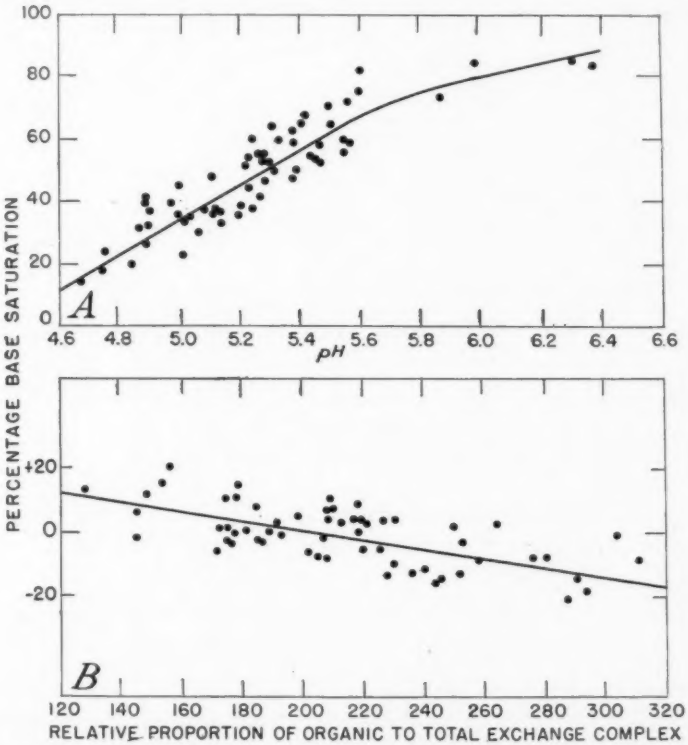

FIGURE 2.—Percentage base saturation (*A*) adjusted for relative proportion of organic to total exchange complex plotted against pH, and (*B*) adjusted for pH plotted against the relative proportion of organic to total exchange complex.

organic to total exchange complex, and consequently it would be expected that soils of the same percentage base saturation would differ in pH value unless the organic and the inorganic exchange complex form acids of the same strength. Since most soils of similar treatment have a fairly uniform carbon-nitrogen ratio, the total nitrogen can serve as an approximate measure of the organic exchange complex. Then, percentage nitrogen divided by the total exchange capacity would give a relative measure of the proportion of the ex-

change complex that is organic. In the Dekalb soils, the index of correlation between percentage base saturation and pH is 0.867. However, the index of multiple correlation between percentage base saturation as the dependent variable, and pH as one independent

TABLE 4.—*The exchangeable calcium, magnesium, and potassium in certain of the pasture soils* [1]

Sample no.	Soil type	pH	Exchangeable bases		
			Ca	Mg	K
			Milli-equivalents	*Milli-equivalents*	*Milli-equivalents*
4	Dekalb silt loam	5.50	5.05	0.70	0.48
20	do	5.38	6.58	.98	.58
21	do	5.24	5.12	.65	.45
27	do	5.86	12.00	1.70	1.00
28	do	5.46	8.10	1.20	.58
38	do	5.32	6.21	.83	.46
39	do	5.29	5.72	.68	.26
45	do	5.06	4.44	.35	.24
48	do	4.75	2.70	.19	.33
51	do	5.01	3.84	.61	.31
53	do	5.31	9.52	1.59	.41
56	do	5.26	4.63	.82	.25
57	do	5.01	2.50	.32	.43
59	do	5.28	7.35	.75	.34
60	do	5.22	8.48	.70	.21
61	do	5.13	6.42	.45	.45
67	do	5.45	6.68	.70	.36
68	do	5.27	5.38	.52	.23
69	do	4.99	5.36	.82	.27
72	do	5.56	3.62	.94	.76
74	do	5.55	3.67	.59	.67
75	do	5.31	3.45	.68	.60
76	do	4.89	3.29	.57	.38
77	do	4.86	4.00	.37	.35
79	do	4.99	4.54	.72	.41
80	do	4.66	1.42	.11	.20
25	Dekalb fine sandy loam	5.12	2.47	.30	.19
26	do	5.02	2.43	.32	.19
34	Dekalb silty clay loam	5.46	7.99	1.23	.21
Average			5.27	.70	.40
103	Hagerstown silty clay loam	6.03	5.05	.74	.51
105	do	5.96	4.88	1.00	.33
109	do	6.82	9.86	.72	.21
112	do	6.87	15.41	.87	.46
113	do	6.55	10.35	3.77	.42
114	do	6.03	7.46	2.00	.35
115	do	6.31	8.75	.82	.40
117	do	6.00	4.21	.53	.20
119	do	5.98	4.99	.47	.27
121	do	6.64	8.20	.85	.29
124	do	6.42	7.67	1.58	.19
125	do	6.47	7.32	.97	.23
126	do	6.31	6.54	.94	.26
Average			7.74	1.17	.32
1	Upshur silty clay loam	5.65	7.91	.73	.80
2	do	5.70	8.57	.86	.95
83	do	5.77	8.30	.46	.22
87	do	5.83	8.54	.51	.35
9	Westmoreland silt loam	5.29	13.06	1.18	.25
91	do	4.92	3.26	.58	.44
37	Elk silt loam	4.96	2.21	.50	.32
49	do	5.68	8.55	.69	.31
32	Pope silt loam	4.98	5.30	1.61	.30
99	do	5.39	8.41	1.18	.20
100	do	5.43	7.88	1.18	.18
Average			7.45	.86	.39
Average all soils			6.35	.85	.38

[1] Exchangeable sodium, based on 18 samples, ranges from 0.02 to 0.14 m. e. per 100 grams of soil, with an average value of 0.07.

variable, with percentage nitrogen divided by the total exchange capacity as the other independent variable, is 0.933. If accurate determinations were made of the ratio of the organic to the total exchange capacity instead of the approximate values used, the index of multiple correlation undoubtedly would be higher than 0.933. The regression curves for this relationship (fig. 2) show that in the Dekalb soils the acids of the organic exchange complex are stronger than those of the inorganic. This means that soils with a high organic-matter content have higher values for percentage base saturation at a given pH value than soils low in organic matter.

With the Hagerstown soils, on the other hand, there is not sufficient variation in the organic-matter content to enable a similar study of the relative strength of the acids of the organic and the inorganic exchange complex.

In view of the fact that a high percentage of the soil magnesium and potassium, especially the latter, is in a nonexchangeable form, whereas the calcium is largely in an exchangeable form, it might be expected that as the soil becomes more acid the exchangeable calcium would be depleted more rapidly than the exchangeable magnesium or potassium. However, there are a number of Dekalb silt loam samples between pH 4.7 and 5.6 in which the equilibrium has not recently and probably never has been disturbed by the use of lime or fertilizer, yet the ratio of Ca:Mg:K in the exchange complex apparently is not affected by the soil reaction. The ratio of exchangeable Ca:Mg:K (on the basis of equivalent weights) averages 83:11:6 in the Dekalb soils and 84:12:4 in the Hagerstown soils (table 4).

TABLE 5.—*Properties and composition of soils from nearby areas supporting different pasture species*

BENT GRASS AND DANTHONIA AREAS

Area and sample no.	Pasture no.	Soil type	pH	Base saturation	Exchangeable bases	PO_4	N	K
				Percent	*Milliequivalents*	*P. p. m.*	*Percent*	*Milliequivalents*
Bent grass areas:								
5	2	Dekalb silt loam	5.11	30	3.64	11.0	0.293	0.25
20	7	do	5.38	42	8.24	26.0	.482	.58
30	10	do	5.38	37	6.24	24.0	.482	.53
69	2	do	4.99	48	6.67	9.5	.249	.27
74	2	do	5.55	52	5.03	12.0	.221	.67
25	8	Dekalb fine sandy loam	5.12	25	2.81	24.0	.329	.19
2	1	Upshur silty clay loam	5.70	57	10.30	15.5	.366	.95
88	27	do	4.95	31	6.91	15.0	.486	.50
Average				40	6.23	17.1	.363	.49
Danthonia areas:								
6	2	Dekalb silt loam	5.07	31	3.26	9.5	.267	.30
21	7	do	5.24	33	6.20	20.0	.464	.45
31	10	do	4.84	16	2.33	18.5	.333	.29
71	2	do	4.89	48	6.90	10.5	.223	.39
75	2	do	5.31	51	5.11	9.0	.192	.60
26	8	Dekalb fine sandy loam	5.02	23	2.91	32.0	.376	.19
3	1	Upshur silty clay loam	5.46	49	7.61	12.5	.274	.27
90	27	do	4.75	15	2.27	13.0	.326	.33
Average				33	4.57	15.6	.307	.35

TABLE 5.—*Properties and composition of soils from nearby areas supporting different pasture species*—Continued

KENTUCKY BLUEGRASS AND BENT GRASS AREAS

Area and sample no.	Pasture no.	Soil type	pH	Base saturation	Exchangeable bases	PO_4	N	K
				Percent	*Milliequivalents*	*P. p. m.*	*Percent*	*Milliequivalents*
Kentucky bluegrass areas:								
4	2	Dekalb silt loam	5.50	55	6.60	16.0	0.330	0.48
22	8	do	7.44	100		1,200.0	.421	
27	9	do	5.86	71	15.25	27.0	.474	1.00
34	13	do	5.46	58	9.57	19.0	.288	.21
67	2	do	5.45	57	7.76	10.0	.254	.36
73	2	do	6.32	82	8.81	23.5	.242	1.64
1	1	Upshur silty clay loam	5.65	54	9.70	18.0	.340	.80
89	27	do	5.05	44	8.30	25.0	.472	.36
109	34	Hagerstown silty clay loam	6.82	97	10.68	14.0	.201	.21
Average [1]				65	9.58	19.1	.325	.63
Bent grass areas:								
5	2	Dekalb silt loam	5.11	30	3.64	11.0	.293	.25
23	8	do	5.41	60	7.14	32.0	.298	.18
28	9	do	5.46	48	9.58	22.0	.475	.58
35	13	do	5.46	61	11.62	15.5	.342	.21
68	2	do	5.27	54	6.28	9.0	.243	.23
72	2	do	5.56	58	5.23	9.5	.189	.76
2	1	Upshur silty clay loam	5.70	57	10.30	15.5	.366	.95
88	27	do	4.95	31	6.91	15.0	.486	.50
111	34	Hagerstown silty clay loam	6.40	83	8.51	10.0	.195	.34
Average [1]				53	7.76	13.4	.324	.48

KENTUCKY BLUEGRASS AND DANTHONIA AREAS

Kentucky bluegrass areas:								
4	2	Dekalb silt loam	5.50	55	6.60	16.0	0.330	0.48
38	15	do	5.32	59	7.57	13.0	.270	.46
53	21	do	5.31	63	11.57	24.0	.384	.41
59	23	do	5.28	50	9.34	24.0	.331	.34
73	2	do	6.32	82	8.81	23.5	.242	1.64
79	25	do	4.99	33	5.46	15.0	.356	.41
64	24	Dekalb silty clay loam	5.50	78	13.91	20.0	.274	.46
24	8	Dekalb fine loam	5.40	50	5.81	36.0	.362	.27
13	5	Dekalb sandy loam	5.54	53	5.80	33.5	.274	.21
16	5	do	5.23	51	4.10	16.0	.214	.26
1	1	Upshur silty clay loam	5.65	54	9.70	18.0	.340	.80
89	27	do	5.05	44	8.30	25.0	.472	.36
8	3	Westmoreland silt loam	5.56	71	16.22	16.5	.406	.30
10	4	do	5.90	72	14.90	24.0	.368	.27
120	39	Hagerstown silty clay loam	6.87	85	10.60	12.5	.177	.24
Average				60	9.25	21.1	.320	.46
Danthonia areas:								
6	2	Dekalb silt loam	5.07	31	3.26	9.5	.267	.30
39	15	do	5.29	54	6.95	11.0	.245	.26
54	21	do	5.37	67	12.22	11.0	.325	.48
62	23	do	4.74	21	3.11	19.5	.264	.32
75	2	do	5.31	51	5.11	9.0	.192	.60
80	25	do	4.66	16	1.98	8.0	.235	.20
66	24	Dekalb silty clay loam	6.37	95	18.06	12.0	.223	.38
26	8	Dekalb fine sandy loam	5.02	23	2.91	32.0	.376	.19
15	5	Dekalb sandy loam	5.27	43	3.59	15.0	.236	.14
17	5	do	4.89	26	1.60	10.5	.157	.12
3	1	Upshur silty clay loam	5.46	49	7.61	12.5	.274	.27
90	27	do	4.75	15	2.27	13.0	.326	.33
9	3	Westmoreland silt loam	5.29	69	14.69	12.0	.376	.25
12	4	do	5.19	60	11.00	16.0	.327	.28
121	39	Hagerstown silty clay loam	6.64	90	9.40	9.0	.135	.29
Average				47	6.92	13.3	.284	.29

[1] Excluding samples 22 and 23, which are abnormal.

SOIL FACTORS DETERMINING THE PERCENTAGE OF KENTUCKY BLUEGRASS AND WHITE CLOVER IN PASTURES

Comparisons Within Pastures

Table 5 gives comparisons of the pH, percentage base saturation, total exchangeable bases, available phosphate, total nitrogen, and exchangeable potassium of soils on which different species are dominant. In all cases the comparisons are made between nearby areas within a pasture where the physical properties of the soil are as nearly alike as possible. It is generally recognized that bentgrasses (*Agrostis* spp.) are tolerant of acid soil conditions, yet in each of the eight comparisons the pH value is higher on the bentgrass areas than on the *Danthonia* areas, although it is true that in some cases the difference is small. Moreover, both the values for percentage base saturation and for available phosphate are higher on the bentgrass areas in all but two cases, and those for total nitrogen are higher in all but one. The differences in total exchangeable bases and in exchangeable potassium are not significant. A comparison of adjacent areas of Kentucky bluegrass and bentgrass shows that in every case the Kentucky bluegrass areas are higher in available phosphate, and in seven of the nine cases, less acid. Since bentgrass requires a more productive soil than *Danthonia*, and since the soil requirements of Kentucky bluegrass are higher than those of bentgrass, it is to be expected that Kentucky bluegrass would have higher soil requirements than *Danthonia:* and in the 15 comparisons, pH is higher in 13 cases, percentage base saturation in 12, total exchangeable bases in 13, available phosphate in 15, total nitrogen in 14, and exchangeable potassium in 12. The question now arises, are these all determining factors, or are some of them merely associated but not limiting factors.

Statistical Analysis of All Pasture Areas Sampled

Analysis by the multiple curvilinear correlation method does not give an accurate measure of the effect of the various soil properties on the botanical composition of the pasture because of the interrelationships involved in the response of the plant to these factors. Nevertheless, it is possible by the use of this method to determine which soil factors are limiting as well as the range within which a particular factor is limiting. A preliminary examination of the data showed that reaction (or percentage base saturation), available phosphate, and total nitrogen apparently were the only chemical properties limiting the percentage of Kentucky bluegrass plus white clover. It should not be inferred, however, that pasture management and climatological factors, as well as the various soil properties affecting penetration and retention of moisture, are not important factors determining plant distribution in permanent pastures. For the most part these samples were collected from areas of moderate to heavy grazing, so there is no adequate comparison of the effect of heavy and light grazing. The climatological differences for the areas within a soil series are not large and, furthermore, are difficult to evaluate. Differences in the slope of the soil, direction of slope, and the depth of surface soil apparently are not important factors within the range studied. However, practically all of the soils sampled had at least 5 inches of surface soil and were on slopes of less than 25 percent. Differences in soil texture appear to be unimportant except in the case

of shaly soils; in such soils moisture appears to be more of a limiting factor. As shown in table 2, however, the range in texture is relatively small.

Since reaction (or percentage base saturation), available phosphate, and total nitrogen were the only chemical properties found to be limiting, the importance of each was studied after removing all samples in which one or both of the other properties were limiting. In addition, certain groups were excluded for the reasons indicated below.

(*1*) *Shaly loam soils* (*three samples*).—On shallow shaly loam soils, moisture often appears to be limiting to the extent that Kentucky bluegrass cannot successfully compete with other plants, even when chemical studies of the soil indicate that the fertility and reaction are favorable.

(*2*) *Areas predominantly bentgrass* (*19 samples*).—It appears that the percentage of Kentucky bluegrass depends to some extent upon whether it is competing with *Danthonia* or with bentgrass. It has already been shown that there is less difference between the chemical properties of soils supporting Kentucky bluegrass and bentgrass than between those supporting Kentucky bluegrass and *Danthonia;* so in the critical range it would be expected that if bentgrass rather than *Danthonia* were competing with Kentucky bluegrass, the percentage of Kentucky bluegrass would be less. One additional sample, which was predominantly Canada bluegrass, was also excluded.

Hagerstown soils.—The Hagerstown soils are well adapted to a study of the relationship between available phosphate and the botanical composition of the pastures because soil acidity is generally not a serious limiting factor. The pH values of these samples vary from 5.68 to 7.44 with corresponding variations in percentage base saturation from 63 to 100. In six samples, however, the total nitrogen content is less than 0.145 percent, and in these cases nitrogen is apparently a limiting factor. In general, exchangeable potassium varies from 0.2 to 0.5 milligram equivalents per 100 g of soil, yet even at the lower range it does not appear to be limiting. On the other hand, it is entirely possible that the amounts of exchangeable potassium may appear adequate for maximum percentages of Kentucky bluegrass and white clover only because available phosphate is a more important limiting factor.

As shown in figure 3, *A*, there is a high correlation between the percentage of Kentucky bluegrass plus white clover in the pasture and the available phosphate content of the soil. The index of correlation for this relationship is 0.901 (*n* is 17, and the probable minimum correlation is 0.79). The regression curve indicates that as low as 18 parts per million of available phosphate are adequate for high percentages of Kentucky bluegrass and white clover. Eighteen parts per million of phosphate corresponds to 13 pounds per acre of phosphorus, assuming that the availability in the 3- to 6⅔-inch layer is the same as in the 0- to 3-inch layer. Since it is obvious from table 3 that the available phosphate is lower in the 3- to 6⅔-inch layer than in the 0- to 3-inch layer, 18 parts per million of available phosphate corresponds to less than 13 pounds per acre of available phosphorus. This value is extremely low as compared with the value of 75 pounds recommended by Truog for general field crops. The difference probably is due to a combination of several factors. In the first place there is, of course, a difference between the available

phosphate necessary to maintain a good stand of Kentucky bluegrass and that required to produce maximum growth. Moreover, these pasture soils are considerably higher in organic matter than the average cropped soils and consequently they are presumably higher in organic phosphorus. The higher content of organic phosphorus probably would tend to compensate for the lower amount of available inorganic phosphate as determined by chemcial methods.

Figure 3, *B*, shows the relationship between the percentages of Kentucky bluegrass plus white clover and the available phosphate

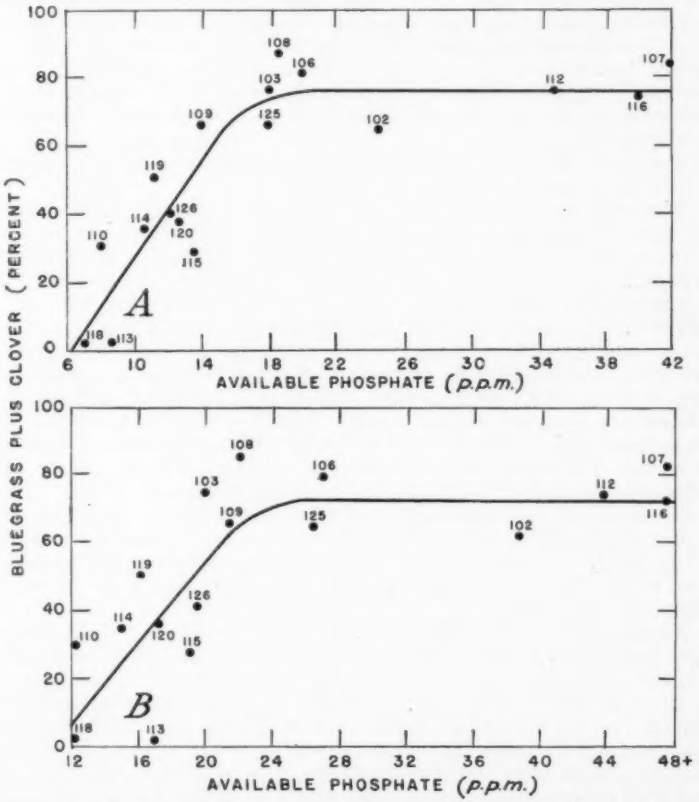

FIGURE 3.—Relationship, in the Hagerstown soil series, between the available phosphate in the soil and the percentage of bluegrass plus white clover in the pasture (*A*), and the same after the 1-year storage period (*B*). Numbers represent soil-sample numbers.

based on the second determinations (i. e., those obtained after the samples were stored for 1 year). It is quite obvious that this correlation is not so high as the one based on the values for available phosphate determined soon after the samples were collected, the index of correlation being 0.782 as compared with 0.901. This would indicate that determinations of available phosphate should be made soon after the soil samples are collected. On the basis of these later determina-

tions, a minimum of 24 parts per million of available phosphate, rather than 18, is required for a good stand of Kentucky bluegrass and white clover, other factors not being limiting.

Dekalb soils.—The effect of the available phosphate content of the soil on the percentage of Kentucky bluegrass and white clover has been shown with the Hagerstown soils. The Dekalb samples cannot be used for similar studies of the effect of available phosphate because in most cases acidity is a limiting factor. On the other hand, these samples are well adapted to a study of the effect of soil reaction on the percentage of Kentucky bluegrass and white clover because after excluding those samples containing less than 18 parts per million of available phosphate, there are still a sufficient number of samples to study the effect of reaction. The Dekalb soils are considerably higher in total nitrogen than the Hagerstown, and in no case does total nitrogen appear to be a limiting factor. The minimum values for exchangeable potassium are approximately the same as for the Hagerstown soils and, similarly, exchangeable potassium apparently is not an important limiting factor.

Figure 4, *A*, shows the relationship between the percentage of Kentucky bluegrass plus white clover and the pH value of the soils. Figure 4, *B*, differs in that percentage base saturation is substituted for pH. A comparison of these two curves shows that in these samples percentage base saturation is a much better measure of the effect of soil acidity than is pH, the index of correlation being 0.800 for pH and 0.945 for percentage base saturation. Thus, differences in the pH of the soil explain 64 percent of the differences in the percentage of Kentucky bluegrass plus white clover, whereas differences in percentage base saturation explain 89 percent. The probable minimum correlations are 0.60 for pH and 0.88 for percentage base saturation. This is in agreement with the findings of Pierre (*17, p. 205*), who concluded that "the hydrogen-ion concentration of soils cannot be considered the direct cause of poor plant growth nor the main factor governing plant distribution or response to liming." On the other hand, "The percentage base saturation of soils is believed to be one of the most important factors in determining the growth of plants on acid soils."

As was stated earlier, there is no adequate comparison of the effect of light and heavy grazing; only two samples were collected from lightly grazed areas, and one of these was not sufficiently productive to support Kentucky bluegrass. Sample 79, on the other hand, had 60 percent of Kentucky bluegrass (table 2) but was lightly grazed, apparently because of the presence of dewberry briars. Since this sample had only 15 parts per million of available phosphate, it was excluded in the correlation studies along with the group containing less than 18 parts per million. Regardless of the phosphate availability, however, the percentage of Kentucky bluegrass was much higher than would be expected on the basis of the pH or percentage base saturation. It is suggested, therefore, that the light grazing may have been a factor which enabled Kentucky bluegrass to maintain a stand as the soil became less productive, whereas under heavy grazing it may have been crowded out by other species. This seems at variance with the conclusion of Hein and Vinall (*14*), who reported that the percentage of Kentucky bluegrass decreased under light grazing and increased under heavy grazing. However, their studies

were conducted on a relatively productive soil, whereas in this case the chemical studies indicate that the soil has become too poor to support a vigorous growth of Kentucky bluegrass. Consequently, a dense turf would not be maintained under heavy grazing and conditions would therefore be more favorable for the intrusion of native grasses and weeds.

In general it seems apparent from figure 4 that for these soils 60 percent base saturation, corresponding to about pH 5.5, is adequate for a good sod of Kentucky bluegrass and white clover, if other factors are not limiting.

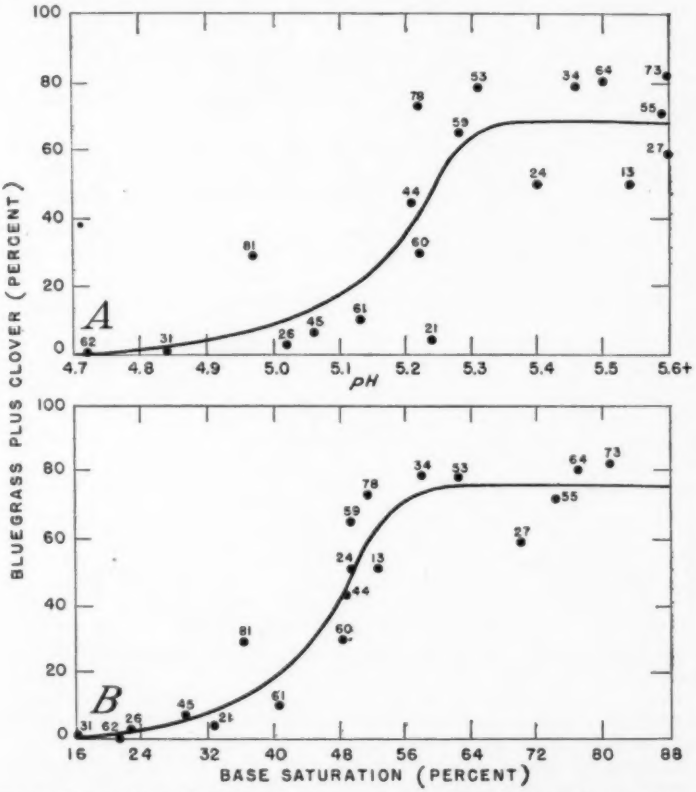

FIGURE 4.—Relationship in the Dekalb series between the percentage of Kentucky bluegrass plus white clover in the pasture and (*A*) the pH of the soil, and (*B*) the percentage base saturation of the soil.

Miscellaneous soils.—There are several soil series which are represented by only a few samples, and consequently each series cannot be studied separately (table 2). The chemical properties of these samples are more nearly like the Dekalb than like the Hagerstown, so they are included with the Dekalb soils in the following studies. The relationship between the percentage of Kentucky bluegrass plus white clover and percentage base saturation is shown in figure 5. For

convenience, the soils other than the Dekalb are designated in the figure. The data indicate that the relationship involving different soil series is not nearly so close as that within a series, the index of correlation being 0.764, as compared with 0.945 for the Dekalb soils alone. It is, of course, to be expected that the relationship would be better when the study is confined to one soil series, since other soil properties, as well as rainfall and elevation, are thereby held more uniform.

SUMMARY AND CONCLUSIONS

The effect of the chemical properties of the soil on the botanical composition of old established pastures was studied on 126 areas located largely on two soil series, the Hagerstown and the Dekalb. The Hagerstown soils are of limestone origin and are among the most productive upland soils in West Virginia, whereas the Dekalb soils are derived from noncalcareous shales and sandstones and are among the least productive.

The soil samples were analyzed for pH, available phosphate, total nitrogen, total exchange capacity, total exchangeable bases, exchangeable potassium, and in some cases exchangeable calcium, magnesium,

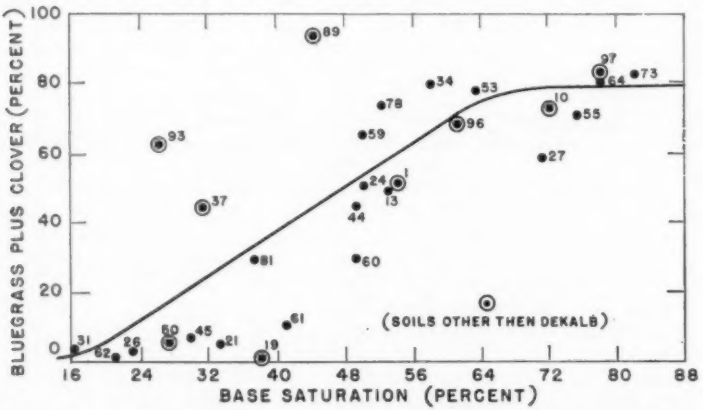

FIGURE 5.—Relationship, in the miscellaneous soils, between the percentage base saturation of the soil and the percentage of Kentucky bluegrass plus white clover in the pasture. Numbers represent soil-sample numbers.

and sodium. The percentage base saturation was calculated from the values for total exchangeable bases and total exchange capacity.

Soil samples stored air-dry for a period of 1 year showed marked increases in available phosphate. In the Dekalb samples the average increase amounted to 78 percent or 13.7 parts per million of available phosphate, as compared with an increase of 40 percent or 7.3 parts per million in the Hagerstown samples. The magnitude of the increase was found to be associated with the organic-matter content of the soil as indicated by total nitrogen determinations. This accounts for the greater increase in the Dekalb samples, which average 0.301 percent nitrogen as compared with 0.179 for the Hagerstown. The original values for available phosphate are apparently a better measure of the availability to the plant than those obtained a year later.

The change in phosphate solubility during storage should be considered when making recommendations for the phosphate fertilization of pastures.

A straight-line relationship was found to exist between the total nitrogen content and the total exchange capacity of these soils, the coefficient of correlation being 0.804 (n is 119, and the probable minimum correlation is 0.74). This high correlation emphasizes the importance of the organic exchange complex and is especially significant since the texture of the soils varied from sandy loams to silty clay loams.

In general, the percentage base saturation of the soils studied is closely associated with the pH value, the coefficient of correlation for the entire group being 0.922 (n is 117, and the probable minimum correlation is 0.90). In the Dekalb soils, however, it was found that with a high ratio of organic to inorganic exchange complex, the percentage base saturation values at a given pH value were relatively high, showing that the acids of the organic exchange complex are stronger than those of the inorganic.

A comparison of the nitrogen content of the 0- to 3- and the 3- to 6-inch layers of Dekalb soils that have been in permanent pasture about 20 to 50 years shows that the 0- to 3-inch layer is 85 percent higher in available phosphate and 65 percent higher in total nitrogen than the 3- to 6-inch layer. The data indicate that approximately 1,000 pounds per acre of nitrogen have been accumulated during this period.

A comparison of samples from the same pastures shows that, in general, soils supporting Kentucky bluegrass are higher in pH, percentage base saturation, total exchangeable bases, available phosphate, total nitrogen, and exchangeable potassium than soils supporting *Danthonia*. A statistical analysis of all samples, however, shows that the primary chemical properties limiting the percentage of Kentucky bluegrass and white clover in the pastures studied are percentage base saturation and available phosphorus.

On shaly loam soils moisture appears to be limiting to the extent that Kentucky bluegrass and white clover may not be able to maintain a stand, although the chemical properties of the soil indicate that conditions are favorable for these species. Moreover, the soils supporting bentgrass are in a higher state of fertility than those supporting *Danthonia*, and consequently when Kentucky bluegrass is competing with bentgrass rather than with *Danthonia*, the available plant food must be greater in order to support a good stand of Kentucky bluegrass.

The effect of any one soil property on the amounts of Kentucky bluegrass and white clover was obtained by determining the index of correlation, after excluding all samples in which other properties were known to be limiting.

In the Hagerstown soils there is a high correlation between the percentage of Kentucky bluegrass plus white clover in the pasture and the amount of available phosphate in the soil. The index of correlation for this relationship is 0.901 (n is 17, and the probable minimum correlation is 0.79).

The studies on the Dekalb soils show that percentage base saturation is a much better measure of the effect of soil acidity on the plant than is pH value, the index of correlation with the percentage of Kentucky bluegrass plus white clover being 0.800 for pH and 0.945 for

percentage base saturation. The probable minimum correlations are 0.60 for pH and 0.88 for percentage base saturation.

The data indicate that the relationship between the chemical properties of the soil and the amounts of Kentucky bluegrass and white clover is closer within a soil series than among different series.

In general, 60-percent base saturation, corresponding to about pH 5.5 for the soils studied, 0.145 percent of total nitrogen, and 0.2-milligram equivalents of exchangeable potassium per 100 g of soil appear adequate for maximum percentages of Kentucky bluegrass and white clover on these soils, if other factors are not limiting.

On the basis of values obtained shortly after the samples were collected, 18 parts per million of available phosphate appear adequate for a good stand of Kentucky bluegrass and white clover, if other conditions are not limiting. On the basis of determinations made 1 year later, 24 parts per million are necessary.

It should be recognized, of course, that the minimum values for percentage base saturation, total nitrogen, and available phosphate necessary for the maintenance of a high percentage of Kentucky bluegrass and white clover in permanent pastures, are lower than the values necessary for the production of maximum yields.

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COLD RESISTANCE OF WINTER WHEAT, RYE, BARLEY, AND OATS IN TRANSITION FROM DORMANCY TO ACTIVE GROWTH [1]

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INTRODUCTION

Winter killing often has been observed in winter wheat and other fall-sown cereals after spring growth has started. Severe injury may result in late winter or early spring from only moderately low temperatures that would cause little or no injury during midwinter. The practical importance of developing varieties that are resistant to killing during early spring is manifested by the serious losses frequently sustained by growers.

Extensive studies of the relative hardiness of winter cereals, particularly varieties of wheat in the hardened condition, have been made by Åkerman (*1*),[3] Newton (*19*), Salmon (*27*), and others. Also a number of workers, including Suneson and Peltier (*30*), Newton and associates (*19*, *20*, *21*), and Martin (*15*) have studied the hardening changes that take place in wheat during the fall, from the active growing condition to the winter condition. In the investigations reported upon here the transition of winter cereals from the dormant winter condition to the active spring condition was studied with respect to the rate of change in cold resistance, the relative hardiness at various stages of early spring growth, and the association of certain conditions in the plants with cold resistance during the transition period.

REVIEW OF LITERATURE

Harvey [4] recently prepared a very extensive and complete bibliography of the low-temperature relations of plants, including annotated references to 3,412 publications in this field. Abbe (*2*) summarized studies made prior to 1894 on the influence of cold on plants.

Salmon and Laude (*28*) have shown that the ability of a variety of winter wheat to survive the winter is of major importance in determining varietal adaptation. This fact is emphasized by Quisenberry and Clark (*24*), who point out that during the 26-year period from 1901 to 1926 an average of about 10 percent of the total winter wheat acreage of the United States was abandoned, largely because of winter injury. Marked differences in hardiness of varieties of winter wheat were shown by Clark, Martin, and Parker (*5*).

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[2] The writer wishes to acknowledge the stimulating suggestions and helpful directions given by Dr. Charles A. Shull, plant physiologist, and other members of the Department of Botany, University of Chicago. Appreciation is expressed to C. W. Nauheim for assistance in collecting data.

[3] Reference is made by number (italic) to Literature Cited, p. 916.

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Martin (*15*) found artificial freezing to be the best laboratory method for measuring the cold resistance of wheat. A close relation between the results of artificial freezing and winter injury in the field was demonstrated by Salmon (*27*). In experiments with oats Mather and Andersson (*17*) found artificial freezing to be a satisfactory way of determining comparative cold resistance and obtained a good correlation between the laboratory freezing tests and field results. Martin (*14*), working during the spring-growth period, found good agreement between injury in the field and injury by artificial refrigeration, and observed that it was possible to measure varietal differences in wheat by artificial freezing in both hardened and slightly hardened plants.

Rosa (*26*) concluded that cold resistance in plants is due to the increased water-retaining power of the cells, which enables them upon freezing to retain a larger proportion of their moisture content in the unfrozen condition.

Hooker (*9*) attributed the ability of plant tissue to hold water unfrozen when the plant is subjected to winter conditions to the pentosans, or even a specific pentosan. Hardy tissues contain less free water and more colloidal water than tender tissues. It has been suggested that the greater water content of tender tissue is due to an excess of free water. A positive correlation between hardiness and bound water was observed also by Lott (*13*).

Akerman (*1*), upon finding a close relation between cold resistance of wheat and its sugar content, developed the view that sugars have an important protective influence. Newton and Brown (*21*) have shown that sugar disappears gradually from winter wheat plants during the winter, the rate of loss being somewhat greater in nonhardy than in hardy varieties. Maximov (*18*) attributed greater endurance to cold to the accumulation of sugars and other soluble carbohydrates in the cell and to an increase in the water-retaining power of the cells in consequence of the accumulation of hydrophilic colloids.

Newton (*19*) found a close relation between the relative hardiness of varieties of wheat, the percentage of bound water, and the hydrophilic colloid content in the press juice of hardened tissues.

The hardening process, according to Harvey (*8*), is brought about by low temperature. During the hardening of wheats Martin (*15*) observed a decrease in moisture content and an increase in total solids in the sap. He also reported a positive correlation in a given variety between quantity of juice expressed and moisture content. Chandler (*3*) found that resistance to low temperature increased with an increase in sap density. As temperature decreased, Constantinescu (*6*) observed increases in total sugar content, osmotic pressure, and dry matter in winter wheat. Janssen (*11*) reported a positive correlation between total soluble carbohydrate compounds and winter hardiness. Dexter (*7*) concluded that hardening of plants is favored by conditions favoring the accumulation or conservation of carbohydrates and other reserve foods and that a high available carbohydrate supply is essential before the cold-temperature reaction of hardening of plants will occur in an efficient manner.

Roemer, Rudorf, and Lueg (*25*) measured total solids in the pressed juice of wheat leaves with the refractometer and found that varietal differences could readily be detected by this method in winter, when the plants were hardened. They found that the concentration of

solids in the juice was higher in cold than in warm weather and that varietal differences were greater in winter than in the spring. They concluded that the refractometer method parallels other methods in determining winter hardiness in varieties of wheat.

Dehydration of the cells is believed by Newton and Brown (*22*) to be the basic cause of the precipitation of proteins which occurs when tissue is killed by freezing. They found that sugar added to press juice decreased the precipitation and stabilized the juice protein.

Tottingham (*31*) found that respiration increased more than photosynthesis with an increase in temperature. Thus the result was a decrease in the carbohydrate-protein ratio. He concluded that temperature becomes the dominant factor in the regulation of metabolism by controlling the equilibrium between certain anabolic and catabolic reactions.

After intensive study of respiration of wheat plants at low temperature, Newton and Anderson (*20*) concluded that at −7° C. the rate of respiration in wheat varieties is inversely proportional to winter hardiness. They found the differentiation was indefinite early in the season but became increasingly sharp as the plants advanced into the fully hardened condition.

Howard (*10*) held that the rest period in plants is induced and maintained by the inhibition of the enzymes due to the accumulation of the products of their work and by cool weather. He attributed growth after the rest period to an increase in enzyme activity. According to Newton and Brown (*23*) the catalase activity of press juice of winter wheat leaves is directly related to the winter hardiness of the varieties.

Nauheim [5] found that the loss of cold resistance of winter cereals in early spring was associated with increase in moisture and decrease in solids. Johnston (*12*) noted that the moisture content of peach buds increased during late winter and early spring and that the relation between moisture and effective temperatures was expressed as a straight-line equation.

MATERIALS AND METHODS

Winter wheat, rye, barley, and oats were grown at Manhattan, Kans., and were hardened outdoors by natural weather conditions. The hardened plants were moved to the greenhouse, where conditions favorable for growth were maintained. The experimental methods employed measured changes that occurred in the plants during the transition from the hardened, nearly inactive winter stage to the unhardened, very active spring stage. The characteristics and habits of growth assumed by the plants in the greenhouse were typical of those normally acquired in the field during the spring. It therefore appears reasonable to assume that the data obtained in these studies represent winter-spring transition conditions that occur normally in the field.

Studies were made with Rosen and Dakold winter rye, Tennessee winter barley, Sporen winter oats, and Kanred winter wheat. A description of the varieties of rye is given by Martin and Smith (*16*) and of Kanred wheat by Clark and Bayles (*4*). Rosen rye, C. I. no. 195,[6] is slightly more winter-hardy under most conditions than the

[5] NAUHEIM, C. W. THE RELATIVE LOSS OF HARDINESS IN WINTER CEREALS WHEN SUBJECTED TO WARM TEMPERATURES DURING WINTER AND EARLY SPRING. Thesis, Kans. State Col. 1934.

[6] C. I. denotes accession number of Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

leading varieties of hard winter wheat. Dakold rye, C. I. no. 175, is very winter-hardy, perhaps as hardy as any known cereal. C. I. no. 3543 barley, used in these experiments, is a selection of Tennessee, a hardy variety of winter barley which is extensively grown. Sporen oats, C. I. no. 2506, is a variety of winter turf oats. Kanred C. I. no. 5146 is a red winter wheat that is relatively winter-hardy and is extensively grown.

The investigations included artificial freezing of hardened plants and of similar plants after they had been kept in the greenhouse for varying lengths of time or at different temperatures. In order to determine the comparative cold resistance in the hardened condition, plants were taken directly to the refrigerator from outdoors. The other plants in some of the experiments were taken into the greenhouse at one time and frozen at intervals thereafter, while in other experiments the plants were taken into the greenhouse at intervals and frozen simultaneously.

Adequate measurements could not be made by freezing all groups of plants at one time, because of too wide differences in cold resistance. Since some of the hardy groups might not be injured at all, while the less hardy groups might be killed entirely, it would have been impossible to measure definite differences in cold resistance among either the most hardy or the least hardy groups. Thus it was necessary so to plan the experiments that no freezing test included groups having more than a moderate range in hardiness.

For the freezing experiments, five plants were grown in 4-inch clay pots, the soil in which was prepared by mixing three parts of silt loam, one part of manure, and one part of sand. They were planted the latter part of September or early in October, which is about the normal time for fall seeding in the field at Manhattan. Soil moisture was maintained at about optimum. The barley and oats were covered with a muslin canvas during the coldest nights, to reduce the danger of winter killing.

The equipment described by Sellschop and Salmon (*29*) was used for the artificial freezing. Briefly it consists of a chamber in which cooling is effected by expansion of carbon dioxide. The temperature within the chamber is thermostatically controlled.

The freezing period was 12 hours, ending either at 8 a. m. or 8 p. m. After treatment, the plants were kept in the greenhouse and usually were observed for injury after 2 to 4 days. Injury was estimated and recorded as percentage of killed tissue in each pot. About 2 weeks after the plants were frozen the percentage of living plants in each pot was recorded. The experimental error was calculated for each experiment either by analysis of variance or by averaging the standard deviations of all the units. A close relation was found between the results expressed as injury and as survival, which agrees with the conclusion reached by Salmon (*27*). Unless otherwise stated, the freezing data are reported as the percentage of tissue killed by the treatment.

Moisture determinations were made with 5 g of fresh tissue which was dried to constant weight in a Freas oven at 95° C. The quantitative determinations of expressed juice were made by placing samples of tissue in a hydraulic press under pressure of 1,660 pounds per square inch, or 115 atmospheres, for 5 minutes. The tests were made in duplicate, with 3 g of green leaves. Each sample was wrapped in enough filter papers to absorb all the juice expressed from the leaves.

Usually six filter papers 9 cm in diameter were used for each sample. The filter papers were weighed before and after absorption of the pressed juice, the leaf tissue being discarded, and the filter papers with the pressed juice being immediately placed in weighing bottles to prevent loss by evaporation. The difference in the weight of the filter papers before and after pressing represented the amount of juice expressed from the sample.

Determinations of the total solids in the plant sap were made with the Abbe refractometer. The sap was obtained with a press devised for this work in which a small representative sample of the plant tissue was placed on a finely perforated plate through which a few drops of the juice were forced under high pressure.

The plants used in determining the moisture content, the quantity of expressed juice, and the solids in expressed sap, were grown outdoors in flats 20 inches square and 4 inches deep. Part of them were moved to the greenhouse at the beginning of an experiment, and samples for the several tests were taken at intervals to measure changes in the plants that might be associated with the progressive loss of hardiness. The soil for the flats was prepared in the same way as that for the pots. The seed was planted between September 27 and 29. About 125 plants were grown in each flat.

EXPERIMENTAL RESULTS ON LOSS OF COLD RESISTANCE

The loss of cold resistance associated with the change from outdoor winter environment to the greenhouse was studied in winter wheat, winter rye, winter barley, and winter oats in 2 years, 1932–33 and 1933–34. Kanred wheat, Tennessee barley, and Sporen oats were used in both seasons; Rosen rye was included the first year and Dakold rye the second.

Duplicate experiments, A and B, were run to obtain data on the rate of loss of hardiness. In each experiment 80 pots of plants were used, 20 for each of the four crops. Of these 20 pots, 4 were not placed in the greenhouse, 4 were placed in it for 12 hours, 4 for 24 hours, 4 for 36 hours, and 4 for 48 hours. The greenhouse was maintained at favorable growing conditions, the temperature averaging 67° F. Then all the 80 pots in each experiment were frozen at the same time at 8° for 12 hours, the ones used in experiment A on January 3 and those used in experiment B on January 8, 1933. The relative cold resistance of the different lots of each crop is shown by the freezing injury reported in table 1. The standard error of the mean was found to be 3.1 percent, from which it may be assumed that differences among the averages greater than 8.8 percent are statistically significant for odds 19:1.

It is apparent that the crops began to lose resistance to cold very soon after their removal to the greenhouse. A marked loss of hardiness had occurred at the end of 24 hours, and small but consistent changes were found within the first 12 hours. Thus the difference in freezing injury during the first 12 hours was 5.5 percent for wheat, 4.5 for rye, 6 for barley, and 2.5 for oats. At the end of 24 hours the differences had increased to 46 percent for wheat, 50 for rye, 53 for barley, and 44.5 for oats. It appears therefore that the change in cold resistance for the period from 12 to 24 hours was highly significant for each of the crops as was also the change from 24 to 48 hours.

A part of the first 12-hour period was required to warm the soil; this may account for the small change during the first period as compared with the second period. A portion of the first period may also have elapsed before the plants responded to the stimuli of the greenhouse environment. The freezing injury increased for all the crops in each of the remaining 12-hour periods, although in no case was the change as great as in the second period.

TABLE 1.—*Cold resistance measured by freezing injury of winter cereals when hardened and after 12, 24, 36, and 48 hours in the greenhouse; frozen at 8° F. for 12 hours*

Crop	Experiment	Percentage freezing injury in plants under different conditions				
		Hardened	After indicated number of hours in greenhouse			
			12	24	36	48
Kanred wheat	A	3	9	49	51	60
	B	3	8	49	59	76
	Average	3	8.5	49	55	68
Rosen rye	A	8	15	53	64	69
	B	4	6	59	68	89
	Average	6	10.5	56	66	79
Tennessee barley	A	15	19	53	66	80
	B	1	9	69	76	90
	Average	8	14	61	71	85
Sporen oats	A	29	35	75	76	85
	B	21	20	64	78	91
	Average	25	27.5	69.5	77	88

In another experiment cold-resistance changes in the first 4 days in the greenhouse were studied for Kanred wheat, Rosen rye, and Sporen oats. The procedure was the same as in the preceding experiment. This experiment was repeated five times between January 23 and February 2, 1933. The average freezing injury for the six experiments is given in table 2. The standard error was found to be 1.28 percent for the values given in the table. From this it may be considered that a difference of 3.6 percent is statistically significant.

TABLE 2.—*Cold resistance measured by freezing injury of wheat, rye, and oats when hardened and after 1 to 4 days in the greenhouse: frozen at 12°–14° F. for 12 hours*

Crop	Percentage of freezing injury in plants under different conditions				
	Hardened	After indicated number of days in greenhouse			
		1	2	3	4
Kanred wheat	8	30	51	63	82
Rosen rye	8	30	42	72	82
Sporen oats	67	73	76	73	94

Rosen rye and Kanred wheat were equally resistant to freezing injury in the hardened condition and after 1 day and 4 days in the greenhouse and were much alike at the other stages. They apparently lost hardiness at about the same rate. Sporen oats was much less resistant than the other crops in the hardened condition and lost resistance more slowly so that after 3 to 4 days it was injured only slightly more than the wheat and rye.

DAILY CHANGE IN COLD RESISTANCE OF KANRED WHEAT THROUGHOUT TRANSITION

The data that have been presented indicate that cold resistance was lost quickly after the plants were placed in the greenhouse where the environment stimulated the winter-spring transition changes. Since considerable resistance to cold still remained after 4 days, additional experiments were made to determine the length of time acquired cold resistance could be retained in such an environment, and to determine the rate of loss over a longer period. The experiments were conducted during January, February, and March 1934. It was found necessary to freeze the plants in three groups since it was not possible to obtain differential freezing injury when plants in all stages of cold resistance from the hardened to the unhardened condition, were frozen simultaneously. One group included hardened plants and those that had been in the greenhouse from 1 to 6 days. Another group included plants that had been in the grrenhouse from 5 to 12 days, and the third, those that had been in the greenhouse from 9 to 16 days. The average freezing injury of the plants in each of the groups is given in table 3.

TABLE 3.—*Daily changes in cold resistance of hardened Kanred wheat for 16 days after transfer to the greenhouse*

Condition of plants and time in the greenhouse (days)	Average [1] percentage freezing injury in—		
	Group 1 frozen at 7° F.	Group 2 frozen at 18° F.	Group 3 frozen at 20° F.
Hardened	5		
In greenhouse:			
1	34		
2	50		
3	66		
4	78		
5	87	43	
6	96	50	
7		60	
8		58	
9		71	41
10		74	44
11		85	40
12		90	46
13			56
14			50
15			53
16			54

[1] Averages for 24 pots in groups 1 and 3 and 12 pots in group 2.

The values given in table 3 are averages of 24 pots in groups 1 and 3 and 12 pots in group 2. The standard errors are 1.6 percent for group 1; 5.8 for group 2; and 4.4 for group 3. Thus differences

necessary for odds as high as 19:1 are 5, 16, and 13 percent respectively in the three groups. Because of the wide difference in cold resistance the first group was frozen at 7° F., the second at 18°, and the third at 20°. The freezing time in each case was 12 hours. The rate of change throughout the entire period is shown in figure 1, the curves for the three separate groups being superimposed on each other so as to give a continuous curve.

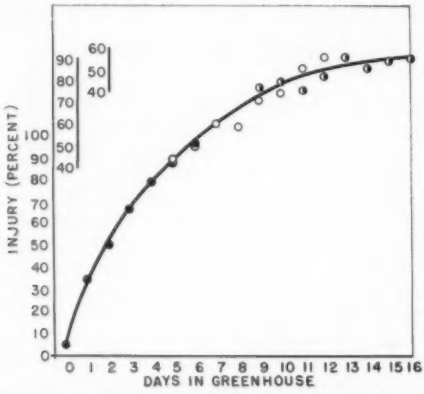

FIGURE 1.—Rate of loss of cold resistance in Kanred wheat throughout a 16-day period in the greenhouse. The plants were frozen in three groups on the basis of the length of time they had been in the greenhouse. The left scale of injury applies to the hardiest group, frozen at 7° F., including hardened plants and those that had been in the greenhouse from 1 to 6 days. The middle scale is for the second group including plants that had been in the greenhouse from 5 to 12 days, which were frozen at 18°, and the right scale is for the third and least hardy group, frozen at 20° after having been in the greenhouse from 9 to 16 days. The curves for the three groups are superimposed on one another so as to give a continuous curve.

It is apparent that the loss of cold resistance was very rapid in the first period, less so in the second, and very slow in the third. After 2 weeks the plants could withstand very little more freezing than if they had been grown continuously in the greenhouse, indicating that nearly all of the resistance to cold acquired outdoors had been lost. In other words, the transition from the hardy winter condition to the nonhardy spring condition had been practically completed.

RELATIVE RATE OF LOSS IN WHEAT AND OATS

An experiment similar to the one just described was made to compare the rates of loss of cold resistance in Kanred wheat and Sporen oats. Hardened wheat and oat plants that had been in the greenhouse from 1 to 7 days were frozen. Three separate tests with each crop were made between January 15 and 28, 1934. The data are shown in table 4.

TABLE 4.—*Relative loss of cold resistance in hardened wheat and oats when placed in the greenhouse at 68° F.*

Condition of plants and time in the greenhouse (days)	Percentage freezing injury for—	
	Kanred wheat, frozen at 7° to 11° F.	Sporen oats, frozen at 17° F.
Hardened	3	12
In greenhouse:		
1	33	16
2	61	29
3	74	47
4	80	51
5	79	64
6	95	76
7	96	84

The injury to wheat increased during the first 3 days from 3 to 74 percent, while the injury to oats increased from 12 to 47 percent. During the next 4 days wheat changed in cold resistance more slowly than oats. Although Kanred wheat, when hardened, is known to be much more resistant to cold than Sporen oats, the difference in the rate of change shown in this experiment would tend to make the two crops more nearly equal in hardiness at certain stages in the transition period.

COMPARATIVE RESISTANCE OF WINTER CEREALS AT INTERVALS DURING TRANSITION

The different rates at which cereals lost cold resistance in the experiments that have been reported suggest that the relative hardiness may vary at different times in transition from the dormant to the active stage of growth. To establish the comparative hardiness at several times in the transition period, wheat, rye, barley, and oats were frozen simultaneously when hardened and also at intervals after transfer to the greenhouse. Thirty-two pots of each of the four crops were moved into the greenhouse at one time, and eight of each crop were frozen immediately to measure the relation of the crops in the hardened condition. Similar lots were frozen after 6, 9, and 12 days to determine the relative cold resistance of the crops at each of those times. The experiment was repeated nine times at each stage of hardiness between January 6 and March 5, 1934; in the course of this work 5,760 plants were tested. Additional plants were tested on the third day in some of the experiments and on the 15th day in others.

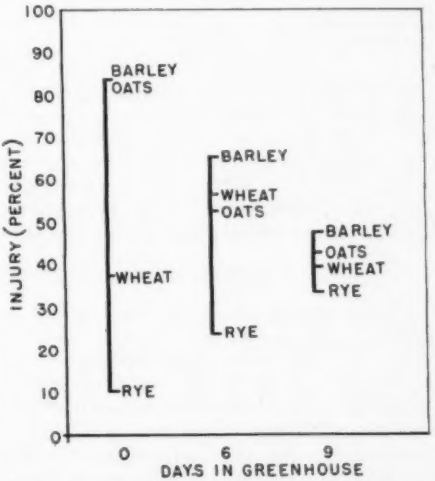

FIGURE 2.—Comparative cold resistance of wheat, rye, barley, and oats when hardened and after 6 days and 9 days in the greenhouse.

The hardened crops differed widely in cold resistance since the average freezing injury of Dakold rye was 10 percent, as compared with 38 for Kanred wheat and 85 percent for Tennessee barley and Sporen oats, as shown in table 5 and illustrated in figure 2. The standard error of this experiment for the values given in the table was 1.65 percent; from this it was found that a difference of 4.7 percent between freezing injuries of crops within a stage is significant for odds of 19:1.

The crops became more nearly equal in cold resistance at each successive test until at the end of 9 days the greatest difference (that between rye and barley) was only 13 percent. Little difference in cold resistance was found when the crops had been in the greenhouse

12 and 15 days. The data show that for these crops in the hardened condition the range of injury was 75 percent, whereas at the end of 6 days in the greenhouse it had decreased to 42 and in 9 days to 13 percent.

Table 5.—*Comparative cold resistance of cereals at intervals in transition from dormancy to active growth, when hardened and after 6, 9, and 12 days in the greenhouse*

Crop	Percentage of freezing injury in plants under different conditions			
	Hardened, frozen at 5°–7° F	After indicated number of days in greenhouse		
		6, frozen at 14°–16° F	9, frozen at 17°–19° F	12, frozen at 19°–21° F
Kanred wheat	38	57	40	50
Dakold rye	10	24	34	39
Tennessee barley	85	66	47	59
Sporen oats	85	53	43	53

Although hardened Sporen oats was much less resistant to cold than Kanred wheat the two crops were not significantly different after having been in the greenhouse 6 days. Due to transition changes the hardy Dakold rye became nearly as susceptible to freezing as Sporen oats in 9 days in the greenhouse. It seems evident therefore that the transition changes proceeded more rapidly in the hardy crops, rye and wheat, than in the less hardy, barley and oats.

RELATION OF TEMPERATURE TO RATE OF LOSS

In the experiments reported in the preceding pages the principal difference between the outdoor and greenhouse environments was one of temperature. Soil moisture was ample in both cases, and the length of the daily light was nearly the same. The quality and intensity of the light, the atmospheric moisture, and other environmental conditions appeared not to have been so dissimilar as to account for the marked losses in cold resistance that were noted during the first few days the plants were in the greenhouse.

In order to determine the effects of temperature specifically an experiment was conducted in which four pots of hardened wheat plants were moved to each of two greenhouses on 7 successive days. The temperature in one of the houses was maintained at an average of 80° F. and that in the other at 60°. On the eighth day eight pots of hardened plants, together with those that had previously been placed in the two greenhouses, were all frozen at the same time. Similar experiments were conducted with rye, barley, and oats. The crops were frozen between January 14 and 18, 1934. The rye was frozen at 4°, the wheat at 7°, the barley at 16°, and the oats at 17°.

As is shown in table 6, the cold resistance decreased more rapidly in the plants maintained at 80° F. than in those held at 60°. The standard error for the values reported in the table was 2.7 percent; thus the smallest difference that is statistically significant for odds of 19:1 is 7.6 percent.

The loss in resistance in the warm house was as great in 1 day as that in the cool house in 2 days. The data for longer periods fluctuate

considerably, but in general the difference in resistance that developed in the first 2 days was continued. It appears therefore that temperature is a major factor in determining the loss in cold resistance and that the rate of change is associated with the amount of heat.

RELATION BETWEEN CERTAIN CONDITIONS IN WINTER CEREALS AND COLD-RESISTANCE CHANGES DURING TRANSITION

Changes in water content, in amount of plant juice that may be expressed with a given pressure in a given time, and in refraction of the plant sap were studied in relation to the cold resistance of the plants during transition from the dormant to the active stage of growth.

TABLE 6.—*Influence of temperature alone on rate of loss of cold resistance in wheat, rye, barley, and oats*

Condition of plants and time in greenhouse (days)	Average percentage freezing injury after greenhouse temperatures of—	
	80° F.	60° F.
Hardened	6	6
In greenhouse:		
1	33	13
2	52	36
3	57	59
4	77	61
5	73	67
6	87	78
7	96	71

The changes were studied in 1933 for 7 days and in 1934 for as long as 15 days after the plants were moved to the greenhouse. For these experiments, plants grown and hardened in flats outdoors were tested at the time they were moved into the greenhouse in February of each year and at intervals thereafter. The samples in 1934 were comparable as to time of sampling and as to the plants tested. In 1933 the samples for water content and expressed juice were comparable, but those for refraction of sap were taken from other flats at another time. In the first experiment the water content and expressed juice were determined in leaves of hardened wheat, rye, and barley and after the plants had been in the greenhouse 1, 2, 3, 5, and 7 days. Similarly, wheat and barley were tested for refraction of sap. In the second experiment water content, expressed juice, and refraction of sap were studied in comparable samples of wheat, rye, barley, and oats when hardened and at 3-day intervals after the plants had been moved to the greenhouse. The data are shown in tables 7 and 8 and are illustrated in figures 3 to 8.

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TABLE 7.—*Water content, expressed juice, and refraction of sap in leaves of cereals when hardened, and after 1, 2, 3, 5, and 7 days in the greenhouse*

Determination and crop	Data for plants under different conditions					
	Hardened	Results after indicated number of days in greenhouse				
		1	2	3	5	7
Water content:						
Kanred wheat, percent	74.5	76.7	80.2	82.7	84.0	85.1
Rosen rye, do	76.2	80.0	81.9	82.6	84.3	84.8
Tennessee barley, do	77.7	80.1	82.6	84.3	84.8	86.0
Average, do	76.1	78.9	81.6	83.2	84.4	85.3
Expressed juice:						
Kanred wheat, do	23.2	25.3	25.6	29.2	32.2	35.8
Rosen rye, do	23.1	26.7	27.1	28.1	30.9	31.8
Tennessee barley, do	23.2	24.1	25.0	29.5	31.8	36.4
Average, do	23.2	25.4	25.9	28.9	31.6	34.7
Refractive index of sap:						
Kanred wheat	1.3440	1.3400	1.3402	1.3401	1.3390	1.3389
Tennessee barley	1.3475	1.3421	1.3415	1.3404	1.3366	1.3372
Average	1.3458	1.3411	1.3409	1.3403	1.3378	1.3381

TABLE 8.—*Water content, expressed juice, and refraction of sap in leaves of cereals when hardened, and at 3-day intervals after transfer to the greenhouse*

Determination and crop	Data for plants under different conditions				
	Hardened	Results after indicated number of days in greenhouse			
		3	6	9	12
Water content:					
Kanred wheat, percent	77.2	81.2	83.5	84.1	84.6
Dakold rye, do	78.2	81.6	84.3	83.6	83.2
Tennessee barley, do	78.3	82.9	84.6	85.4	86.1
Sporen oats, do	74.9	79.1	80.4	86.1	83.8
Average, do	77.2	81.2	83.2	84.8	84.4
Expressed juice:					
Kanred wheat, do	25.1	31.7	34.8	38.4	45.4
Dakold rye, do	28.8	33.4	34.3	37.8	41.3
Tennessee barley, do	27.0	33.3	36.4	43.8	49.2
Sporen oats, do	24.8	30.0	32.0	37.7	44.4
Average, do	26.4	32.1	34.4	39.4	45.1
Refractive index of sap:					
Kanred wheat	1.3483	1.3380	1.3395	1.3367	1.3351
Dakold rye	1.3450	1.3400	1.3404	1.3369	1.3358
Tennessee barley	1.3472	1.3375	1.3380	1.3356	1.3354
Sporen oats	1.3533	1.3407	1.3402	1.3364	1.3349
Average	1.3484	1.3391	1.3395	1.3364	1.3353

WATER CONTENT OF PLANTS

Barley contained slightly more moisture than rye or wheat at comparable stages throughout both experiments. Wheat had a little less moisture than rye when hardened, and this difference was maintained for 2 days in the greenhouse. After this period the two crops contained nearly equal amounts. The water content of the oats was less than for any of the other crops during the first 6 days in the greenhouse.

The water content of wheat, rye, and barley increased at daily intervals for the first 3 days in the greenhouse, the average change being greatest on the first day and less each day thereafter. Tests made at 3-day intervals show an increase in percentage of water during the first period amounting to 3.4 for rye, 4.0 for wheat, 4.2 for oats, and 4.6 for barley and an increase about one-half as great during the next 3 days. The change from 6 to 9 days was less regular although in general the moisture content increased. There was practically no change in moisture after 9 days, as was shown by tests made 12 and 15 days after the plants were placed in the greenhouse.

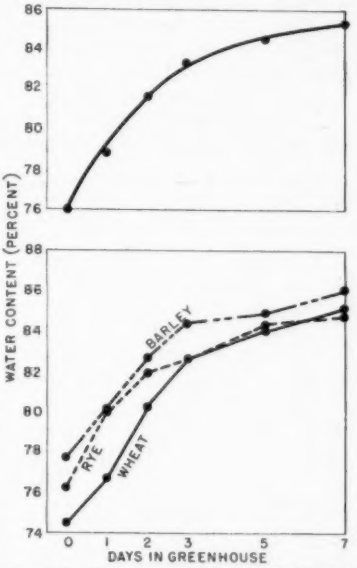

FIGURE 3.—Rate of increase of water in leaves of cereals when hardened, and when transferred to the greenhouse. The upper curve is fitted to the average data.

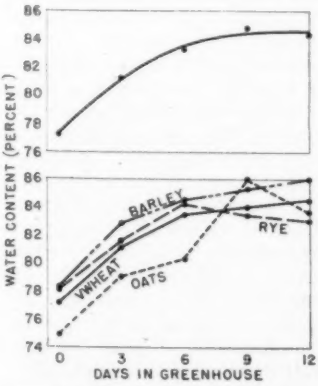

FIGURE 4.—Water content of leaves of cereals when hardened, and at 3-day intervals after being placed in the greenhouse. The upper curve is fitted to the average data.

Representative samples taken at intervals showed that the rate of increase of water in plants and the rate of decrease of cold resistance were similar during the first few days that plants were in the greenhouse. After about 9 days, however, the moisture content remained nearly constant, whereas the plants continued to lose resistance although at a slower rate. It might be assumed that the increase in moisture explained the loss of cold resistance during the first 9 days, but some other cause must be sought to account for subsequent changes.

QUANTITY OF EXPRESSED JUICE

The amounts of juice expressed from the leaves increased in every case with

the length of time the plants were in the greenhouse. In general, the increase was somewhat less in rye than in the other crops which were nearly equal. The smoothed curve drawn to fit the average percentage of expressed juice for all crops is essentially a straight line in both experiments, indicated a uniform rate of increase. Results of other experiments indicated that the original rate of increase was maintained as long as 15 days after hardened plants were placed in the greenhouse.

A comparison of figures 5 and 6 with figures 3 and 4 shows that whereas the quantity of expressed juice continued to increase at its original rate the increase in water content was less after the first 3 days and practically ceased at the end of 9 days. In other words, the increase in moisture was curvilinear, whereas that in expressed juice was linear.

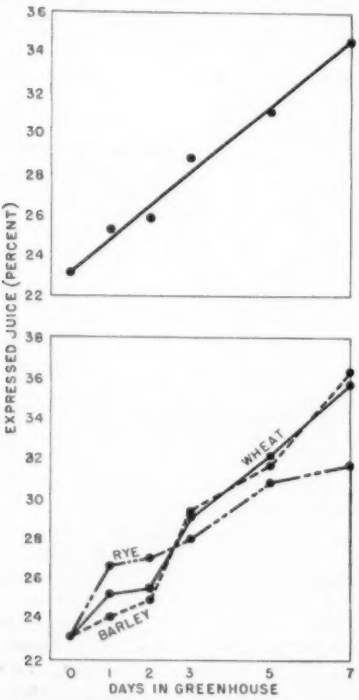

FIGURE 5.—Increase in the amount of juice expressed from leaves of cereals when hardened, and when transferred to the greenhouse. The upper curve is fitted to the average data.

Changes in expressed juice during the first part of the period may be explained as the result of increase in the water content of the tissue. However, since water remained constant during the latter part of the transition, some other factor or factors are evidently involved. Increase in expressed juice and decrease in cold resistance progressed simultaneously during the transition.

REFRACTION OF PLANT SAP

The refraction of the sap was determined as a measure of the relative amounts of total solids in the juice of the plants. The refractometer readings indicate a marked decrease in solids of wheat and barley during the first day that plants were in the greenhouse, as illustrated in figure 7. Although the data fluctuate somewhat there was a definite downward trend in refraction values after that time.

Each of the cereals included in the experiment in which tests were made at 3-day intervals, showed a large reduction in the concentration of solids in the sap during the first 3-day period in the greenhouse. The results of tests at daily intervals suggest that most of this change probably took place during the first day. The reduction in the average refractometer readings was more than twice as much in the first 3 days after the plants were moved to the greenhouse as in the next 9 days, indicating a further but more gradual downward trend in solids. In other experiments it was found that no significant reduction in solids took place after hardening plants had been in the greenhouse 9 days.

Differences in refraction, indicating reductions in total solids of the plant sap, were associated with the increases in water content that have been presented. Most of the change with respect to both solids and water content took place within the first 6 days and very little after the ninth day that the plants were in the greenhouse. Concentration of solids in the sap was not associated with the amount of expressed juice, which, as has been shown, increased at a linear rate throughout the transition.

DISCUSSION AND CONCLUSIONS

Temperature is probably the major factor influencing hardiness changes of winter cereals in the field, although light and moisture are of some importance. In the experiments reported here the significant changes in the artificial environment were primarily changes in temperature. Moisture was maintained at about the optimum and therefore probably was not a differential factor except as its utilization might have been influenced by temperature or perhaps other factors.

Light conditions in the greenhouse are known to be different from those outdoors, but in these experiments the plants that were directly compared were either subjected to the same light conditions or were in different light for so short a time that probably the experimental data were not materially influenced. The same may be said regarding the influence of biological conditions, which are known to be different in the greenhouse and outdoors in winter. Under field conditions these factors might change concomitantly with hardiness in early spring. The small amount of soil to be affected by the temperature change also accounts in part for the quick response of plants in the experiments. It appears reasonable to assume that in these experiments the transition changes occurred more rapidly but otherwise were reasonably comparable with what takes place in the field when the plants change from winter dormancy to active spring growth. In the field the transition probably requires as much as 1 or 2 months, whereas in the greenhouse the plants lost nearly all of their acquired cold resistance in 2 weeks.

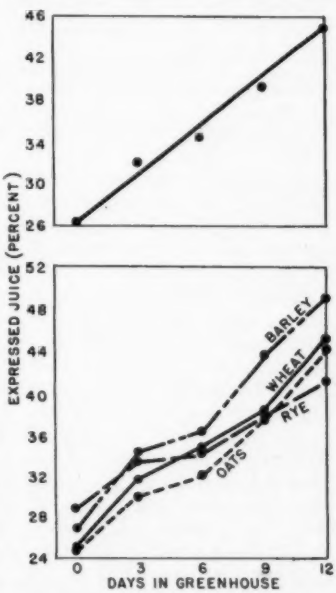

FIGURE 6.—Increase in the amount of juice expressed from the leaves of cereals when hardened, and at 3-day intervals after being placed in the greenhouse. The upper curve is fitted to the average data.

The results indicate that the rate at which a crop loses resistance to cold is roughly proportional to the degree of hardening. Thus a fully hardened plant will change rapidly when the environment becomes favorable for growth, and as resistance is lost the rate of change will decrease.

The studies indicate that the moisture content of plants increases as they lose their hardiness to cold which is the reverse of the water changes occurring while plants become hardened to cold as reported by Newton and Brown (*21*). The increase in pressed juice during the first 3 to 5 days may be explained as associated with the increase in moisture. A different explanation, however, is necessary to account for the subsequent increase of pressed juice which took place without a corresponding increase in water. Colloidal changes resulting in the liberation of bound water afford a logical explanation and are suggested as the probable reason for the relatively high amount of pressed juice as compared with the moisture content of the plants during the latter part of the transition changes.

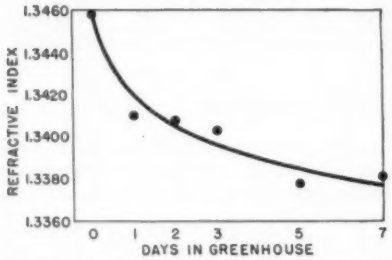

FIGURE 7.—Reduction of total solids in leaves of hardened wheat and barley after transfer to the greenhouse as measured by the refractive index of the sap.

In general, the quantitative changes with respect to solids appear to be associated inversely with changes in water content. This suggests that the phenomenon is chiefly one of dilution brought about by the increasing amount of water in the tissue. However, there is indication that the solids were reduced more during the first day than might be accounted for by the increase in water. The greenhouse environment may have stimulated respiration, with the consequent utilization of solids before an equivalent production of solids was brought about by photosynthesis, the temporary net result of which would be a lower solid content than would be caused by dilution alone.

Investigations of Rosa (*26*) and others have shown that changes which occur while plants acquire hardiness are principally dependent directly or indirectly upon water changes. The present investigations indicate that when plants lose hardiness under the stimulation of favorable environment the changes in cold resistance also are associated with moisture changes. The loss of cold resistance for the entire transition period may be explained on the basis of water conditions, assuming that bound water was changed to free water. Such a change would make more water available for plant

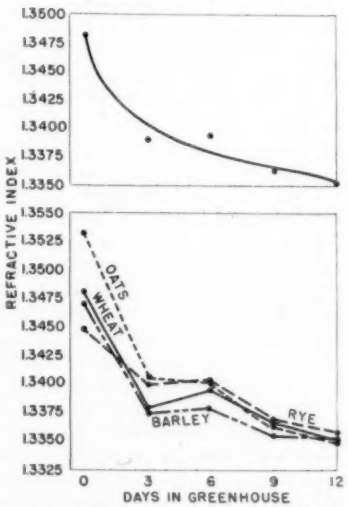

FIGURE 8.—Total solids in leaves of cereals when hardened, and at 3-day intervals after being placed in the greenhouse as measured by the refractive index of the sap. The upper curve is fitted to the average data.

growth without increasing the total water content of the tissue. Thus there might be an increase in the amount of available water corresponding with a decrease in cold resistance until the plant had lost all of its acquired hardiness.

SUMMARY

Changes in cold resistance during transition from dormancy to active growth were studied in winter cereals including wheat, rye, barley, and oats for two seasons, 1932–33 and 1933–34. The crops were planted in the fall in pots or flats, were grown outdoors and hardened by natural winter weather. The transition changes were induced when winter-hardened plants were transferred to a greenhouse where a favorable growth environment was maintained. Relative cold resistance and changes in resistance were measured by artificially freezing the plants at various stages in the transition. Changes in water content of the plants, expressed juice, and refraction of plant sap were studied in relation to changes in cold resistance.

Transition under the control provided in the experiments was faster but otherwise apparently comparable to winter-spring transition in the field. Temperature is thought to have been the chief factor influencing the rate of transition.

The change in cold resistance was found to proceed at a decreasing rate except for a short period of about 12 hours immediately after the plants were placed in the favorable growth environment. This initial time was apparently needed for the soil to warm and for the plants to respond to the temperature. However, as soon as the plants were stimulated into activity their cold resistance decreased very rapidly. The rate of change was greatest during the first part of the transition and gradually became slower until after 2 weeks little change was taking place.

Dakold rye was found to be considerably more resistant to cold than Kanred wheat, which in turn was much more resistant than Tennessee barley and Sporen oats in the hardened condition. However, when the crops had been in the favorable growth environment of the greenhouse 9 days little difference in cold resistance remained among them. All of the crops had lost resistance, and evidently the hardy rye had lost more than the others and wheat more than barley and oats.

Water content of the plants increased and total solids in the sap decreased during the transition. The changes were rapid at first and then slower until about the ninth day, after which little change took place with respect to either condition.

The amount of juice expressed from leaves increased at a constant rate throughout the transition period, suggesting that a change of bound water to free water continued after the maximum water content was attained.

Cold-resistance changes were negatively associated with water content, refraction of sap, and pressed juice during the first half of the transition period and similarly associated with pressed juice during the last half of the period.

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COMPARISON OF THE COLD RESISTANCE OF SEVERAL VARIETIES OF WINTER WHEAT IN TRANSITION FROM DORMANCY TO ACTIVE GROWTH[1]

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INTRODUCTION

A recent study by the author (*5*)[3] relative to the cold resistance of winter cereals during transition from dormancy to the active stage of growth suggested that varieties of a crop may differ in the rate at which hardiness is lost in the winter-spring transition. Since considerable winter-killing occurs in early spring when temperatures are only moderately low, it is important that wheat and other fall-sown cereals be spring-hardy as well as winter-hardy. The relative cold resistance in the hardened condition is well established for many of the older and for some of the newer varieties of winter wheat. The comparative hardiness during transition from the dormant condition of winter to the active growing condition of spring is less well known. The study reported in this paper was made to determine the differences between varieties of winter wheat with respect to the rate of loss of hardiness and the comparative cold resistance at intervals in the winter-spring transition.

REVIEW OF LITERATURE

A review of the literature dealing with winter hardiness, particularly as it relates to transition changes, has been given by the writer (*5*). Changes in the relative hardiness rank of varieties of wheat during the winter were noted by Suneson and Peltier (*7*) and were attributed to hardening adjustments. Anderson and Kiesselbach (*1*) suggest differential adjustment to environmental conditions among varieties of wheat as a possible explanation for occasional reversals of varietal hardiness in different seasons under field conditions. Hill and Salmon (*4*) noted that varieties of wheat when artificially frozen reacted differently, the type of reaction depending upon whether the plants were field-hardened or only slightly hardened.

In a study of the Montmorency cherry, Gardner (*3*) found variations in cold hardiness of flower buds at different stages in their development. Susceptibility to freezing injury at any of the stages was not closely correlated with the degree of differentiation or development that had been attained, nor was susceptibility at one stage correlated with that at another stage.

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[2] The writer wishes to acknowledge the stimulating suggestions and helpful directions given by Dr. Charles A. Shull, plant physiologist, and other members of the Department of Botany, University of Chicago.

[3] Reference is made by number (italic) to Literature Cited, p. 925.

MATERIALS AND METHODS

The experimental methods were in general the same as those used by the author (*5*) in a study of different winter cereals in the transition period. In the present investigation six varieties of winter wheat (*Triticum aestivum* L., syn. *T. vulgare* Vill.) planted in late September were grown in pots out of doors at Manhattan, Kans. In midwinter, when the plants probably had attained their maximum resistance to cold, eight pots of each variety were transferred to the greenhouse and the plants were artificially frozen. At the same time other pots were transferred to the greenhouse and similar groups of the six varieties were frozen at the end of 1, 2, 3, 4, 6, and 10 days. In this way the relative cold resistance of the varieties was directly compared at intervals during transition to the active stage, which was stimulated by the favorable growth environment maintained in the greenhouse. These tests were repeated between January 19 and 29, 1935. The varieties, which are described by Clark and Bayles (*2*), were Minturki, C. I. No. 6155;[4] Kanred, C. I. No. 5146; Quivira, C. I. No. 8886; Tenmarq, C. I. No. 6936; and Blackhull, C. I. No. 6251, which are varieties of hard or semihard red winter wheat, and Harvest Queen, C. I. No. 6199, a soft red winter wheat.

The relative injury expressed as an index was determined by a method similar to the one used by Quisenberry (*6*) in which both the estimate of frozen tissue and the percentage survival were taken into account.

EXPERIMENTAL RESULTS

The comparative freezing injury of the six varieties in the hardened condition and at intervals after the plants were transferred to the greenhouse is reported in table 1. The data permit direct comparisons only in the same column; that is, between varieties that were frozen at the same time.

TABLE 1.—*Comparative cold resistance of varieties of wheat measured by freezing injury when hardened and at intervals after transfer to the greenhouse*

Variety	Average index of freezing injury at different stages						
	Hardened	After indicated number of days in greenhouse					
		1	2	3	4	6	10
Minturki	72	69	80	82	77	72	75
Kanred	76	69	80	85	82	69	65
Quivira	79	77	82	82	80	75	73
Tenmarq	80	75	82	82	76	70	72
Harvest Queen	83	76	81	77	74	60	59
Blackhull	85	81	87	84	82	74	75
Average	79	75	82	82	79	70	70

The standard error for the values given in table 1 is 0.64 percent, from which it was found that within a stage any difference between varieties as great as 1.8 percent is significant for odds of 19:1. The results are illustrated by the plants in figure 1 and are shown graphi-

[4] C. I. denotes accession number of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

cally by the varietal curves in figures 2 and 3. The rate-of-loss curve for wheat which the author (*5*) derived experimentally was used as the basis for the general trend in figures 2 and 3. The varietal curves were located by first superimposing upon the rate curve the average

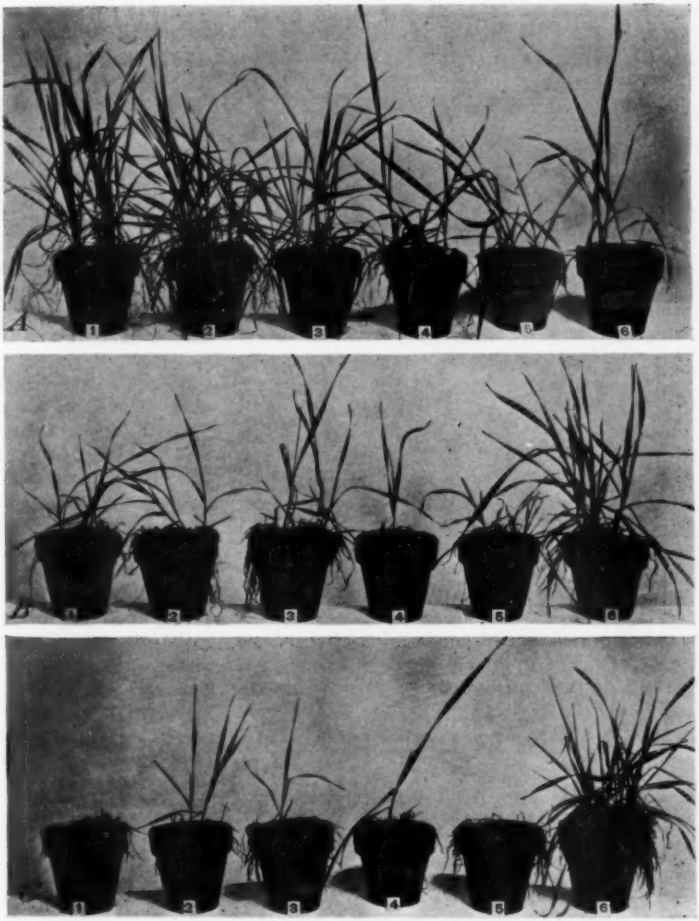

FIGURE 1.—Comparative recovery of six varieties of wheat frozen at three transition stages: *A*, Frozen in the hardened condition; *B*, frozen after being in the greenhouse 6 days; *C*, frozen after being in the greenhouse 10 days. Pot no. 1 is Minturki; no. 2, Kanred; no. 3, Quivira, no. 4, Tenmarq, no. 5, Blackhull, and no. 6, Harvest Queen. Photographed about 7 weeks after freezing.

injury index at each stage in the present experiment and then locating the position of each variety by measuring its experimental deviation in terms of scale deviations.

In the hardened condition the most cold-resistant variety was Minturki, followed in order by Kanred, Quivira, Tenmarq, Harvest

Queen, and Blackhull. Quisenberry [5] has furnished data showing the field survival of these varieties in winter-hardiness nursery tests at a considerable number of stations in the Great Plains area from 1920 to 1935. In these tests Harvest Queen was included for 57 station years, Quivira for 116, Tenmarq for 181, and the others for more than 250. The relative average survival was 118 for Minturki, 103 for Kanred, 87 for Harvest Queen, 84 for Quivira, 83 for Tenmarq, and 79 for Blackhull. Thus it appears that the artificial freezing tests gave essentially the same results as extensive field experiments in measuring the relative hardiness of these varieties. The slightly higher standing of Harvest Queen in the winter-hardiness nursery tests may have been due to its superior spring hardiness, which was not a factor in the artificial experiments with hardened plants.

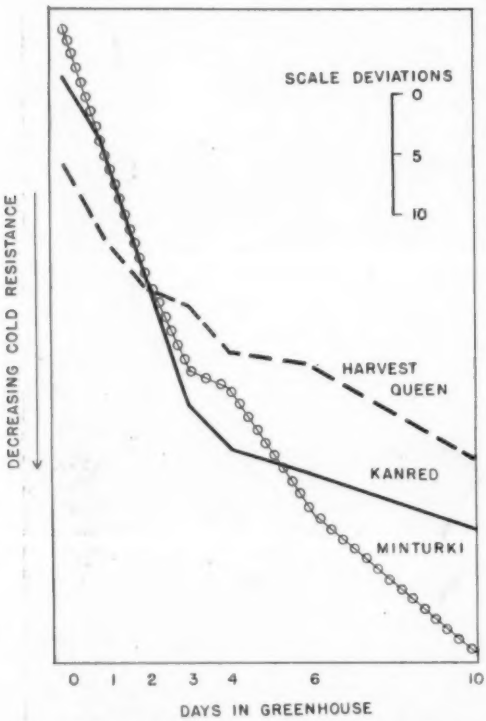

FIGURE 2.—Relative cold resistance of Minturki, Kanred, and Harvest Queen, showing reversal of varieties in transition from dormancy to active growth.

At the end of the first day in the greenhouse the order of the varieties was about the same as that of the hardened plants at the beginning of the experiment. After 2 days the varieties were about equally resistant except Blackhull, which was less hardy. At the end of 3 days Harvest Queen possessed the greatest resistance; the other varieties were nearly alike in this respect. Thus in 2 or 3 days after transfer to the greenhouse, varieties which had differed greatly in cold resistance became about equally hardy owing to different rates of transition.

The rate of transition in Quivira and Tenmarq was about the same, and since these varieties were similar when hardened, they did not differ much at any time during the 10-day period after transfer to the greenhouse. At the end of 6 days Blackhull appeared to be slightly hardier than Quivira. Although Minturki was the most resistant variety at the beginning of the experiment, transition apparently proceeded fast enough to make it less resistant after 10 days than the other varieties except Blackhull, which it equaled in hardiness.

[5] Personal letter.

The relative cold resistance of Minturki, Kanred, and Harvest Queen at the different stages illustrates varietal reversal in hardiness (fig. 2). Because of the slow rate of change in Harvest Queen it was more resistant than the other varieties at the end of 3 days and continued to be significantly hardier thereafter. Minturki, on the other hand, changed from the hardiest to the least hardy of the three varieties within 6 days after transfer to the greenhouse, while Kanred was intermediate both when hardened and at the end of 6 and 10 days after transfer.

The relatively slow rate of change in Harvest Queen has been shown in other studies. In one series of experiments hardened plants of Kanred and Harvest Queen were placed in the greenhouse for 3 consecutive days. On the fourth day the hardened plants and plants of both varieties previously taken to the greenhouse were artificially frozen at the same time. Thus a direct comparison of cold resistance was made among the four stages and between the varieties. The experiment was conducted 10 times between January 18 and February 6, 1933. The average survival of plants is shown in table 2.

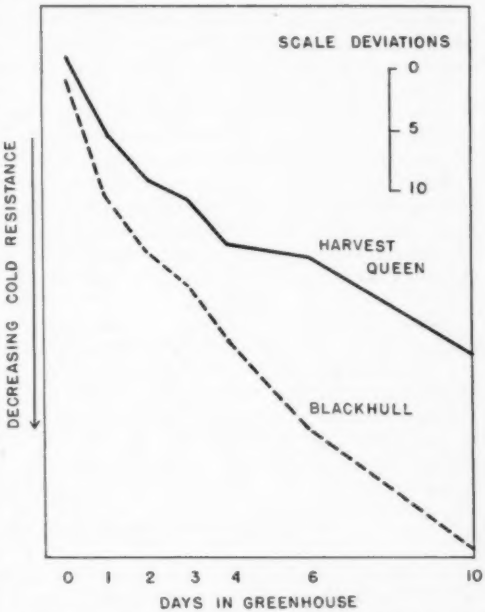

FIGURE 3.—Relative cold resistance of Harvest Queen and Blackhull, illustrating slower transition in the variety possessing the greater midwinter hardiness.

TABLE 2.—*Changes in the relative cold resistance of Kanred and Harvest Queen during transition as shown by artificial freezing when hardened and after 1, 2, and 3 days in the greenhouse*

Variety	Percentage survival of plants in different conditions			
	Hardened	After indicated number of days in greenhouse		
		1	2	3
Kanred	79	51	12	3
Harvest Queen	70	52	24	16

In the hardened condition the difference was 9 percent in favor of Kanred. After 1 day in the greenhouse the resistance of the two

varieties was about the same, but at the end of 2 and 3 days the differences in favor of Harvest Queen were 12 and 13 percent, respectively. The standard error of these experiments was 1.7 percent, from which it was determined that differences greater than 4.8 percent among the values reported in the table are statistically significant. Comparisons may be made among the different stages as well as between the varieties.

In another study during January and February 1934, comparable plants of Minturki and Harvest Queen were artifically frozen at the same time in nine experiments. The average survival of hardened plants of Minturki was 67 percent and of Harvest Queen 51 percent, a difference of 16 percent in favor of Minturki. When the plants were frozen after having been in the greenhouse for 6 days, the survival of Minturki was 63 percent and that of Harvest Queen 68 percent, a difference of 5 percent in favor of Harvest Queen. Thus during 6 days of greenhouse environment the relative resistance of the varieties was reversed. The high statistical significance of the varietal change is shown by the fact that the standard error of the experiment was 2.7 percent, from which it was found that a difference of 7.6 percent has odds of 19:1.

The experiments indicate a tendency for the hardy varieties to change faster during transition than the less hardy ones. However, the results with Harvest Queen and Blackhull illustrated in figure 3 show that transition was slower in the hardier variety. In that case the superiority of Harvest Queen at the beginning of the experiment is shown by a difference of 2 in the freezing index. The difference had increased to 5 at the end of the first day, to 6 the second, 7 the third, 8 the fourth, 14 the sixth, and to 16 the tenth day.

DISCUSSION AND CONCLUSIONS

Changes in the relative cold resistance of several varieties of winter wheat were found in the transition from the dormant to the active stage of growth. Certain varieties that possessed a marked degree of resistance when hardened were not superior, and in some cases were inferior, in this respect several days after spring growth began. Although in general the hardiest varieties lost resistance to cold most rapidly in the favorable growth environment of the greenhouse, the reverse was true in the comparison of Harvest Queen and Blackhull. It is apparent, therefore, that the rate at which cold resistance is lost in varieties of winter wheat in the winter-spring transition is not necessarily associated with the degree of cold resistance in the hardened condition.

Winter-killing losses in wheat during the spring may be reduced by the development of varieties with superior resistance after spring growth starts. No physiological reason is known which would prevent the possibility of finding or developing a hardy variety of winter wheat that will retain a relatively high degree of resistance into the spring growth period, and thus be spring-hardy as well as winter-hardy. The characteristic of slow change in cold resistance from winter to spring has been given little consideration, but with more study it seems probable that among the hardy varieties now known one or more may be found to be highly resistant in early spring as well as in winter. If such a search fails, it should be possible to combine

midwinter hardiness with spring hardiness by crossing such a variety as Harvest Queen with varieties that are highly resistant in midwinter.

No evidence was found in these investigations which indicated a relation between time of maturity and rate of change in cold resistance in the winter-spring transition. It might be thought that early-maturing varieties, because of the shorter time required for them to reach maturity would quickly lose their resistance to cold when the transition changes begin. However, the short time for spring growth apparently is not antagonistic to the maintenance of cold resistance. Quivira ripens 2 or 3 days earlier than Tenmarq, but loses its cold resistance at about the same rate. Kanred is about 2 days earlier than Minturki, but loses its resistance more slowly. Minturki and Harvest Queen ripen at about the same time and later than the other varieties studied. These varieties represent the extremes in rate of change in cold resistance, Minturki changing most rapidly and Harvest Queen most slowly. An explanation for the lack of association between time of maturity and rate of transition may possibly be found in the hypothesis that developmental changes in the life cycle of the plant can proceed independently of cold-resistance changes when spring growth is initiated.

SUMMARY

The comparative cold resistance of six varieties of winter wheat—Minturki, Kanred, Quivira, Turkey, Blackhull, and Harvest Queen—was studied during transition from the winter to the spring stage of growth which was induced by transferring naturally hardened plants in the winter from outdoors to the greenhouse.

Although the loss of cold resistance was usually more rapid in the varieties possessing greater midwinter hardiness, the contrary was also found.

Harvest Queen lost its resistance to cold more slowly than any of the other varieties studied, and thus it retained a relatively high degree of resistance into the spring-growth stage. This character is probably important in protecting the crop against injury from early spring freezes and may well be considered in the improvement of winter wheat.

No relation between rate of transition and time of maturity was found among the varieties studied.

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THE DEVELOPMENT OF THE OAT PANICLE [1]

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INTRODUCTION

Oats (*Avena sativa* L.) differs from the other commonly grown small grains by having an inflorescence in the form of a panicle, while the inflorescences of wheat, barley, and rye are spikes. The panicle consists of a main axis with subdivided branches grouped in clusters (half whorls) at the nodes of the main axis. The arrangement of the clusters or half whorls is alternate and the spikelets are pediceled. On the other hand, the spike is an unbranched inflorescence in which the spikelets are sessile on the main axis.

A panicle differs from a spike in the plan of differentiation and development, as well as in form. However, it is not the purpose of this paper to compare or contrast the development of the panicle with the development of the spike, but to illustrate and describe the principal stages in the formation of the oat panicle and flower.

Few descriptions of the development of the oat panicle have been published. Cannon (*4*) [2] studied the spikelet development of *Avena fatua* L., describing and illustrating various stages in the development of the flower and flower parts. He also studied the formation of the male and female gametophytes, fertilization, and the subsequent development of the caryopsis. The description of the development of the oat panicle given by Noguchi (*6*) is brief and the paper contains only three figures. In addition to other grasses, Arber (*1*) has discussed the morphology of several forms of *Avena*.

MATERIALS AND METHODS

The methods used in taking the photomicrographs in this article are similar to those already described (*2*, *3*).

Plants were grown in the field and greenhouse. They were sampled from time to time to obtain successively advanced stages of development. The panicles were dissected for study and photographing.

DESCRIPTION OF PANICLE DEVELOPMENT

The oat stem, like that of barley and wheat (*2*, *3*) passes through two stages in its development. In the first stage the growing point remains short, the leaf initials differentiate, leaves grow, and tiller buds develop in the axils of the leaves at the base of the stem. During the second stage the internodes of the stem elongate, and the branches, spikelets, and flower parts differentiate and develop.

Two growing points (pl. 1, *A* and *B*) show the first stage in the differentiation and development of an oat stem. The growing point in plate 1, *A* was removed from the stem of a plant showing two leaves.

[1] Received for publication Jan. 18, 1937; issued July 1937. Contribution from the Department of Agronomy, Illinois Agricultural Experiment Station.

[2] Reference is made by number (italic) to Literature Cited, p. 932.

These two leaves and the third leaf initial have been removed to show the growing point and the position and size of the remaining leaf initials. The fourth leaf initial partly encloses the growing point, the fifth leaf initial is seen as a ridge across the growing point, and the growing point itself appears as a smooth, rounded projection above the fifth leaf initial (pl. 1, *A*, l_4, l_5, and *gp*).

A more advanced stage in the development of a leaf initial is presented in plate 1, *B*, l_3. The growing point with the fourth leaf initial appearing as a ridge across it, can be seen through the slit between the leaf margins. As growth continues one leaf margin laps over the other, and the blade becomes rolled.

An oat panicle, as above defined, is a many-branched determinate inflorescence consisting of a main axis from which arise lateral axillary branches which are grouped on alternate sides of the main axis at its nodes. The main axis and each of the lateral branches terminate in a single apical spikelet. The main axis is therefore a determinate inflorescence. The branches have been designated as branches of the first, second, or third order depending upon their point of origin, i. e., whether they arise from the main axis (first order) or from the lateral branches (second or third order).

Previous to the differentiation of the branches of the panicle, the growing point elongates, but the elongation is not so marked as in barley or wheat. This difference between oats and barley or wheat lies, probably, in the difference in the number of nodes on the main axis of the inflorescence. The average number of half whorls of branches on the panicle of some oat varieties, according to Fore and Woodworth (*5*), may range from 5 to 7, while a wheat or barley spike may have from 7 to 20 or more nodes. The averages mentioned vary according to variety and growth conditions.

Panicle formation is first indicated by the appearance of single, lateral, alternate projections (pl. 1, *C*, and *D*, b_1) arising in the axils of leaf initials (pl. 1, *C* and *D*, *l*) beneath the apex of the growing point (pl. 1, *C* and *D*, *t*). At first one, two, and later, several projections can be seen (pl. 1, *D*). These are the primordia of the branches of the first order.

The sequence of differentiation of the branch primordia of the different orders can be traced in plate 1, *C* to *F*, inclusive. The differentiation of the branches of the first order has just been described. As the branch primordia of the first order increase in size at those nodes where many lateral branches are found, branch primordia of the

EXPLANATORY LEGEND FOR PLATE 1.

A. Leaf initials and growing point of an oat plant in the two-leaf stage: l_4, Fourth leaf initial; l_5, fifth leaf initial; *gp*, growing point. × 40.

B. Leaf initial nearly enclosing the growing point: l_3, Third leaf initial. × 40.

C. First stage of panicle development: *l*, Leaf initial; b_1, branch initial, first order; *t*, tip of main axis. × 35.

D. First stage of panicle formation, showing several branch initials: *l*, Leaf initial; b_1, branch initial, first order; *t*, tip of main axis. × 35.

E. A panicle at the beginning of the formation of branches of the second order: *l*, Leaf initial; b_2, branch initial, second order; *t*, tip of main axis. × 35.

F. A panicle at the beginning of the formation of branches of the third order: b_3, Branch initial, third order; *e*, empty glumes; fl_1, initial, first flower; *t*, tip of main axis. × 35.

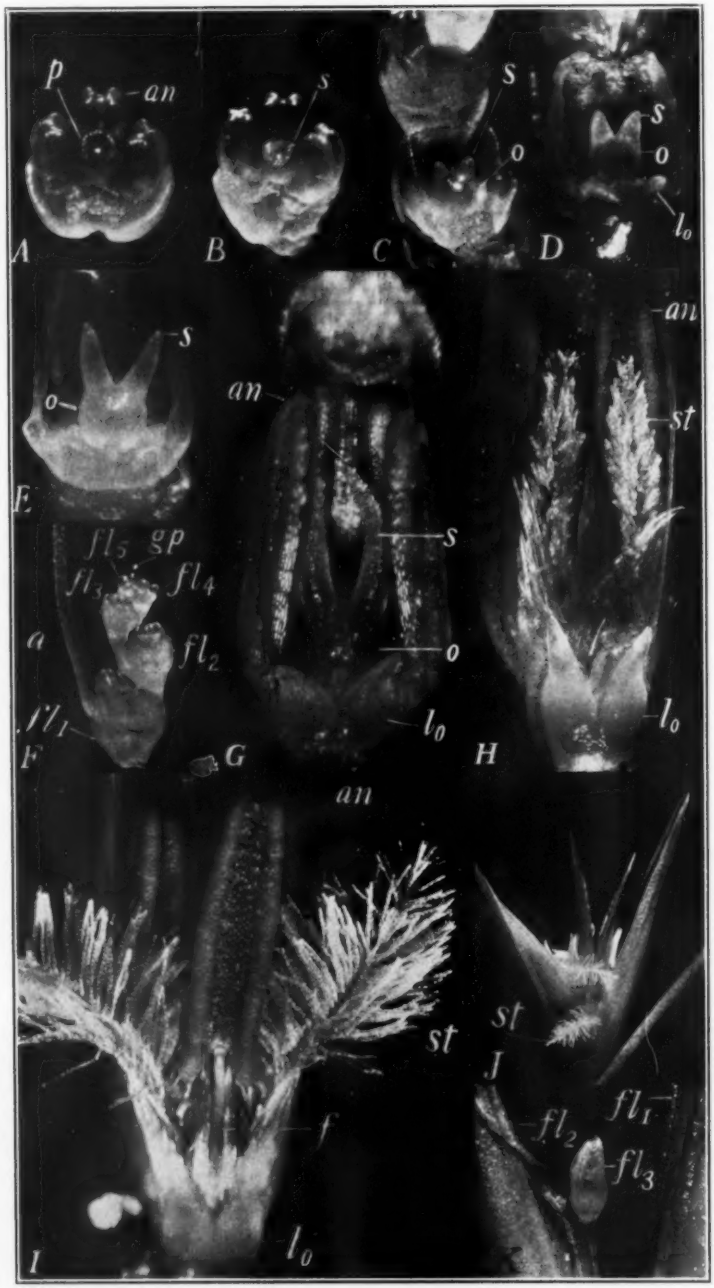
G. A panicle at the beginning of spikelet differentiation: *e*, Empty glume; *g*, lemma; fl_1 and fl_2, initials of the first and second flowers. × 35.

H. The apical spikelet of the central axis, very much enlarged: *e*, Empty glume; *g*, lemma; *an*, anther; fl_3 and fl_2, initials of the second and third flowers. × 55.

I. A panicle showing the relative stages of spikelet development. Empty glumes partly enclose the spikelets: *c*, Collar; *e*, empty glumes. × 20.

J. A panicle showing part of the spikelets enclosed by the empty glumes. The empty glumes have been removed from the apical spikelet of the main axis: *c*, Collar; *e*, empty glumes; fl_1 to fl_5, first to fifth flowers. × 20.

FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.



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second order appear beneath the apex and on alternate sides of the first (pl. 1, *E*, b_2). In turn and in the same manner, primordia of the branches of the third order arise from the second (pl. 1, *F*, b_3).

All the primordia of the lateral branches of the various orders arise in the axils of leaf initials (pl. 1, *C*, *D*, and *E*, *l*). The leaf initials can be clearly seen at the basal nodes of the main axis (pl. 1, *D*, and *E*, *l*). The leaf initials become successively less distinct from the base of the main axis upward to the tip, and likewise, they are less distinct on the branches of the second order.

It should be noted that all branch primordia arise beneath the apex of the parent axis (pl. 1, *C* to *F*). The apex of the branch primordium is the region from which the spikelets differentiate; therefore, new branches arise subapically from the parent axis. Branches elongate between the spikelet and their attachment to the parent axis.

Spikelet differentiation begins first with the spikelet at the tip of the central axis (pl. 1, *F*, *t*) and proceeds basally in succession at the tips of the primordia of the branches of the first order. At the nodes the sequence of spikelet differentiation is (1) branches of the first order, (2) branches of the second order, and (3) branches of the third order. To generalize, those branch primordia that differentiate first are the first to show the differentiation of spikelets.

The beginning of the sequence of spikelet differentiation can be seen in plate 1, *G*, by noting the more advanced stage of differentiation of the spikelet at the tip of the panicle in comparison with that of the two just below it. The branches at the base of the panicle have not yet shown any evidence of spikelet differentiation. Dehiscence occurs in the same order as indicated for spikelet differentiation.

Differentiation of the empty glumes is the first indication of spikelet development (pl. 1, *F* and *G*, *e*). The pair of empty glume initials first appear as prominent ridges, one slightly above the other and each half encircling the branch primordium just beneath the apex (pl. 1, *F*, *e*). The meristem from which flower initials are formed is irregular in outline and extends above the empty glume initials. The empty glumes grow and enclose the developing flowers (pl. 1, *I* and *J*, *e*).

Within the spikelet the flowers differentiate acropetally. The flowers are alternate and attached to a short rachilla (pl. 1, *H*, *J*, and pl. 2, *F*). Flower primordia first appear as protuberances beneath the apex of the growing point above the empty glume initials (pl. 1, *F*, fl_1, *G*, fl_2, and *H*, fl_3). The more basal flower is always more advanced in its development than those above it.

In oats the basal flower and the next one above it are usually fertile, but the third flower does not often produce a kernel. While stamens and pistils differentiate in nearly all the flowers, those stamens

EXPLANATORY LEGEND FOR PLATE 2.

A. An early stage of pistil and anther development: *p*, Pistil; *an*, anther. × 50.
B. Anthers and an oat pistil at the beginning of the differentiation of the styles: *s*, Style initial. × 50.
C. A pistil of oats at the beginning of the elongation of the styles: *o*, Ovary; *s*, style. × 35.
D. A later stage of pistil development: *lo*, Lodicules; *o*, ovary; *s*, style. × 35.
E. A pistil of oats showing elongation of the styles and enlargement of the ovary: *o*, Ovary; *s*, style. × 40.
F. A spikelet of oats, empty glumes removed, to show the position and development of the flowers and awn on the first flower: fl_1 to fl_4, First to fourth flowers; *a*, awn; *gp*, growing point. × 20.
G. An oat flower, one anther removed, with the styles covered with papillae, the primordia of the stigmatic branches: *lo*, Lodicules; *o*, ovary; *s*, style; *an*, anther. × 40.
H. An oat flower, one anther removed, showing the development of the lodicules and stigmatic branches: *lo*, Lodicules; *st*, stigma: *an*, anther. × 20.
I. A fully developed oat flower: *lo*, Lodicules *f*, filament *st*, stigma *an*, anthers. × 15.
J. Unfertilized oat flowers which have opened for pollination: *st*, Stigma. × 1½.
K. Sterile flowers: fl_1 to fl_3, First to third flowers. × 8.

and pistils in all the flowers above the second flower (pl. 1, *J*, fl_3 and fl_4, and pl. 2, *F*, fl_3 to fl_5) usually remain small and rudimentary. In plate 2, *K*, fl_3, the rudiment of the third flower is shown. The remainder of the infertile flowers can be found in the folds of the lemma of the third flower.

The parts of the flower differentiate acropetally. First the lemma and then the palea appear as transverse ridges across the flower initial (pl. 1, *G*, *g*, and *H*, *g*). Soon the anther initials appear as small papillae above the glume initials (pl. 1, *H*, *an*) and finally the pistil differentiates from the meristem between the anthers at the apex of the growing point.

Anthers first appear as papillae upon the mersitem above the flowering glume initials. Very early in the development of the anther the four chambers or locules can be identified. Even before the stage shown in plate 2, *A*, the anthers have separated from the meristem beneath them and filaments have formed. From this stage, as far as external appearances indicate, little change occurs in the anthers except an increase in size.

At the time the three papillae or anther initials appear, a fourth papilla, the pistil initial, can also be seen. At first the pistil shows no change except an increase in size.

Differentiation of the pistil begins with the formation of a ridge (pl. 2, *A*, *p*). The ridge does not at first completely encircle the pistil initial and is more prominent on the side next to the lemma. A papilla, the primordium of the ovule, can be seen in the opening between the ends of the crescent-shaped ridge.

Pistil development is continued by the extension of the ridge entirely around the growing point, enclosing the ovule initial. The margins of the ridge on either side, opposite the laterally placed anthers grow more rapidly than any other portions of the ridge. These two rapidly growing points are the style initials (pl. 2, *B*, *s*).

Increases in the length of the style initials, in the size of the ovary, and the closing of the opening above the ovule are shown in plate 2, *C*, *D*, and *E*. The differentiation and development of the ovule cannot be followed in these illustrations, but the various stages of ovule development have been adequately described by Percival (*7*) for wheat.

The stigmatic branches are the last of the parts of the pistil to differentiate. They first make their appearance upon the styles as papillae (pl. 2, *G*), increase in length (pl. 2, *H*, *st*), finally attain full size and are covered throughout their length with projections which function as lodging points for pollen grains (pl. 2, *I*, *st*).

Some of the stages in the development of the lodicules are shown, beginning with plate 2, *D*, *lo*. In the specimens shown in the photomicrographs of the earlier stages of flower development (pl. 2, *A*, *B*, *C*) the lodicules were destroyed when the lemma was removed to expose the pistil. The lodicules first appear as blunt projections located on either side of the flower at the inner margins of the palea. They increase in size and become rounded at the base and pointed at the tip as shown in plate 2, *H*, *lo*, after which there is very little change.

The chief function of the lodicules is to force the lemma and palea apart and open the flower at anthesis by becoming turgid and thus increasing in size. This function is illustrated in plate 2, *J*, which is a spikelet taken from a plant grown in the greenhouse. Many times

under certain greenhouse conditions viable pollen is not produced and unfertilized flowers open day after day over a considerable period of time.

SUMMARY

A study of the morphological development of the oat panicle was made by dissecting the growing points and panicles from stems in different stages of development. The principal stages of development are shown in photomicrographs.

An oat stem passes through two stages of development. In the first stage leaves and tillers are produced and in the second stage the internodes of the stem elongate and the panicle and its parts differentiate and develop.

Panicle formation is first indicated by the appearance of single, lateral, alternate projections arising in the axils of leaf initials beneath the apex of the growing point. These projections are the primordia of the branches of the first order.

Branches of the second and third order are produced from the parent axes in the same manner that the branches of the first order are produced from the main axis.

Spikelets differentiate from the tips of the branch primordia. Spikelet differentiation begins first at the apex of the main axis and proceeds basally on the branches of the first order and in sequence on the branches of the second and third orders.

The empty glumes are the first of the spikelet parts to differentiate. The flowers of a spikelet differentiate acropetally.

Flower parts differentiate in the following order: Lemma, anthers, palea, lodicules, and pistil.

Ovary, styles, and stigmas is the order of differentiation of the parts of the pistil.

Since the main axis and all branches terminate in spikelets, a panicle can be called a determinate inflorescence.

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PHYTOPHTHORA ROT OF HONEYDEW MELON[1]

By C. M. TOMPKINS, *assistant plant pathologist, California Agricultural Experiment Station*, and C. M. TUCKER, *plant pathologist, Missouri Agricultural Experiment Station*[2]

INTRODUCTION

On September 5, 1935, a rot of Honeydew melon fruits (*Cucumis melo*. L. var. *inodorus* Naud.), caused by *Phytophthora capsici* Leonian (*5*),[3] was observed in part of an extensive planting near Modesto, Calif. The crop was a total loss within the diseased area, involving approximately 2 acres. Visits to other sections of the San Joaquin Valley where Honeydew melons are grown commercially failed to reveal further evidence of the disease. An investigation of the disease, with special reference to cause, factors favoring infection, and host range, seemed desirable because of the economic importance of this and other cucurbitaceous crops grown in the interior valleys of California.

DISEASE FAVORED BY WET SOIL AND HIGH TEMPERATURES

Phytophthora rot of Honeydew melon occurred on heavy, waterlogged soil during the season of prevailing high temperatures. The infested area, lower than the rest of the field, had been improperly graded and lacked adequate drainage outlets. Frequent and heavy irrigations during the latter part of the growing season, necessitated by crop requirements, caused the soil to become waterlogged. Excess water accumulated in small, shallow pools, in and between the rows, and some plants were partly submerged. High temperatures and the contact of the fruits with the wet soil established ideal conditions for infection. The disease did not occur elsewhere in the same field where drainage facilities were good.

SYMPTOMS OF THE DISEASE

In this disease of the Honeydew melon plant, only the fruits are susceptible to natural infection by *Phytophthora capsici*. Both immature and mature fruits, if in contact with or near the surface of the soil, may be attacked. The disease is comparable to a rot of watermelon fruits, recently described by Brown and Evans (*1*) in Arizona and attributed by them to *P. cactorum*.

Two types of incipient lesions may arise after infection occurs—(type 1) small, brown spots, 1 to several millimeters in diameter, with an irregular margin (fig. 1, *A*) which, upon enlarging, may give rise to somewhat larger brown lesions with a water-soaked, outer margin (fig. 1, *C*), or large, slightly zonate, brown, water-soaked lesions

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[2] Grateful appreciation is expressed to Prof. Ralph E. Smith and Dr. M. W. Gardner of the California station for helpful suggestions and assistance.

[3] Reference is made by number (italic) to Literature Cited, p. 944.

(fig. 1, *D*); (type 2) small, water-soaked lesions, 1 to several millimeters in diameter (fig. 1, *B*), which rapidly increase in size to form large,

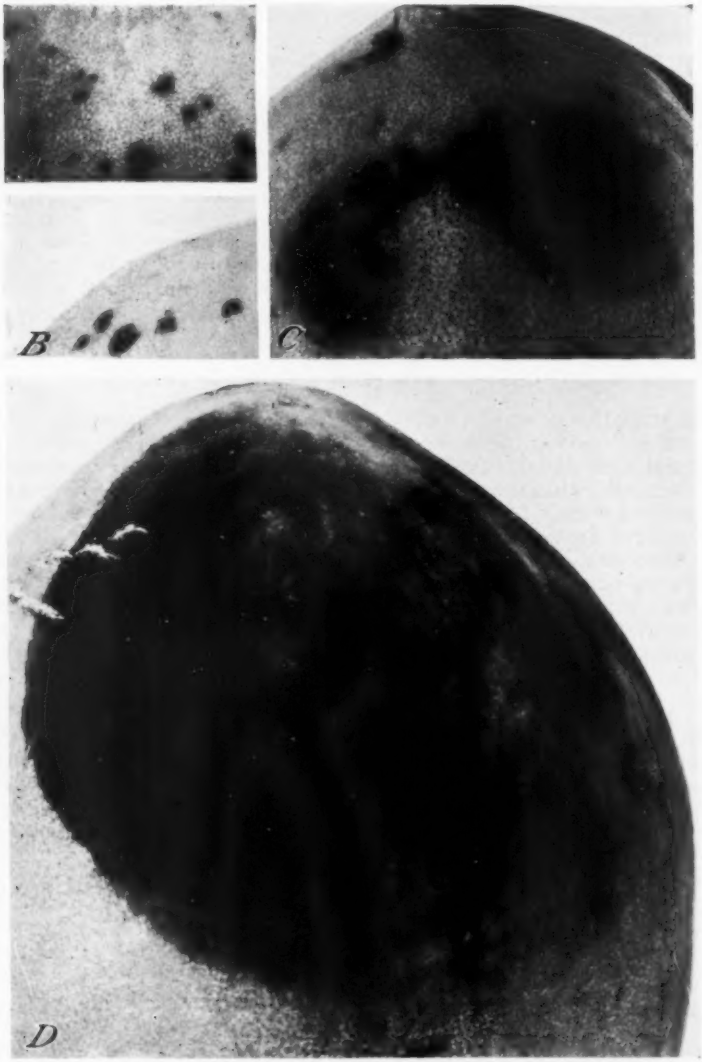

FIGURE 1.—Symptoms of phytophthora rot of Honeydew melons: *A*, Incipient infection showing as small brown spots; *B*, incipient infection showing as small, water-soaked areas; *C*, brown lesions, and brown lesions surrounded by water-soaked areas which arise from incipient brown spots shown in *A*; *D*, slightly zonate, brown, water-soaked lesions arising from incipient brown spots shown in *A*.

water-soaked areas (fig. 2). Of the two types mentioned, the latter is of more common occurrence.

Lesions vary in number on individual fruits from a few to many (fig. 1, *A*, *B*, *C*), but ultimately some of them may fuse. Frequently the water-soaked lesions are covered with a dense, closely adpressed, grayish-white, nonzonate, velvety mycelial mat which contains

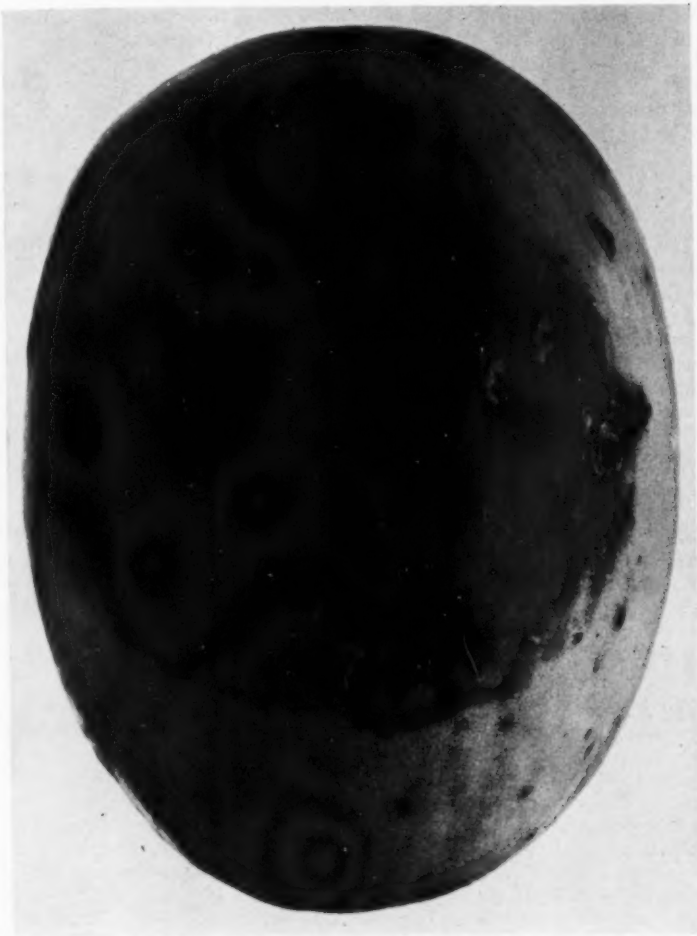

FIGURE 2.—Water-soaked lesions on mature Honeydew melon resulting from incipient infection as shown in figure 1, *B*.

sporangia. In advanced stages of the disease, lesions are slightly sunken in appearance.

Internally, healthy tissues of diseased fruits are sharply delimited from the invaded, water-soaked area, but there is no change in color of the lesion at its margin such as characterizes the advancing edge of

lesions in the roots of sugar beet (*Beta vulgaris* L.) produced by *Phytopthora drechsleri* Tucker (*10*). The fungus spreads rapidly within the fruit, or fleshy berry or pepo (*4*), from the epicarp or exocarp through the spongy parenchymatous cells of the mesocarp and into the endocarp. The decaying tissues have a soft, watery, mushy consistency and lack odor. Sometimes aerial mycelium of the fungus is found in the cavity of the fruit as well as on the surface of the seed coats, to which reference is later made.

While infected fruits show no indication of cracking of the epidermis and underlying tissues, yet they lack mechanical firmness and are easily broken upon removal from the vines.

THE CAUSAL FUNGUS, PHYTOPHTHORA CAPSICI

ISOLATION

The fungus was readily isolated from naturally infected Honeydew melons by removing aseptically small tissue fragments from the advancing, internal part of a lesion, planting on malt-extract agar (*7*) in Petri dishes, and incubating at room temperature. After 48 hours, pure cultures of the fungus were established on agar slants by transferring hyphal tips from the edge of the colonies. A total of 56 tissue plantings was made from 14 diseased fruits, from which 55 colonies were obtained. One pure culture from each fruit was reserved for further study; of these, 13 were identified as *Phytophthora capsici* and 1 as *P. drechsleri*.

RELATION TO HOST TISSUE

Small blocks of tissues from artificially infected Honeydew melons were fixed in formal-acetic-alcohol. Sections were cut 15μ in thickness and stained with Magdala red and fast green. *Phytophthora capsici* was found to be well distributed throughout diseased areas but was confined to the intercellular spaces. There was no indication of intracellular invasion.

IDENTITY

The isolations of *Phytophthora capsici* from Honeydew melons were very similar in most characteristics. All produced abundant aerial mycelium and sporangia in oatmeal agar tubes and in flasks of moist corn meal; none developed chlamydospores in culture. In plate cultures on Difco corn-meal agar the growth was smoothly circular from the inoculum, usually cottony and homogeneous without the development of tufts of hyphae; however, in two isolates sectoring occurred, conspicuous areas in which the hyphae radiated from the center, giving the mycelium a combed appearance; the fungus spread over the medium more rapidly in the sectors. Some transfers from the sectors continued to produce the divergent type of growth, and others continued developing sectors of both types. Leonian (*6*) has demonstrated the marked tendency toward sectoring exhibited by other species.

All isolations produced sporangia on oatmeal agar or hyphae transferred from pea broth to distilled water or to Petri's solution (fig. 3, (*A–D*). The sporangia from solid media ranged in size from 26μ to 55μ by 18μ to 38μ, with average dimensions of about 42μ by 31μ. Those produced after 3 days on hyphae transferred from pea broth

to Petri's solution measured 28μ to 67μ by 21μ to 48μ, averaging about 48μ by 34μ. When transferred from pea broth to distilled water and incubated 3 days at 20° C. (*6*), the hyphae produced larger sporangia somewhat earlier and more abundantly than in Petri's solution, rang-

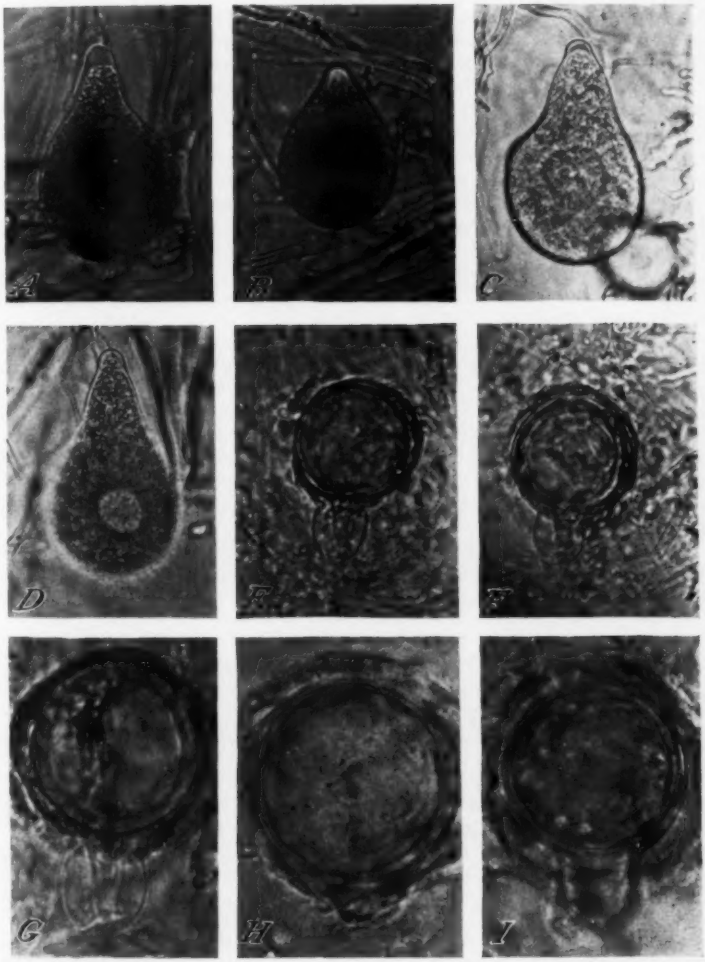

FIGURE 3.—*Phytophthora capsici*. *A–D*, Sporangia developed on hyphae transferred from pea broth to distilled water. × 460. *E–F*, oogonia, oospores, and antheridia from oatmeal agar cultures. × 460. *G*, oogonium partially cleared in a lactophenol solution. × 780. *H–I*, oogonia cleared in a potassium hydroxide solution. × 780.

ing from 31μ to 71μ by 24μ to 57μ, with an average of about 54μ by 39 μ.

The sporangia were papillate in all cultures. On oatmeal agar they were mostly sphaero-limoniform and fairly uniform in shape. Sporangia developed in liquid cultures were larger and more fre-

quently irregular in shape, with a marked tendency toward elongation in the apical region; two or more papillae were occasionally present. These differences suggest the "hydrosporangia" and "aerosporangia" described by Curzi (*2*) from infected tissues in water and in the air. Germination occurred by the development of germ tubes or by zoospores which were differentiated within the sporangium. Chlamydospores were not observed, but occasional undifferentiated ovoid to subspherical hyphal swellings were found in oatmeal-agar cultures.

Ten of the thirteen isolates produced oogonia and oospores in oatmeal agar cultures incubated 4 months at 15° C. The oogonia were usually embedded in the medium and were most abundant at the upper, dried end of the slope. They were subspherical and thin-walled, but the wall was generally encrusted with a dark-brown material, apparently composed of irregular crystals, which increased the apparent diameter of the oogonia and obscured the antheridia. Mounting in a lactophenol preparation caused partial clearing, and soaking in concentrated potassium hydroxide solution removed the deposit (fig. 3, *G–I*). The oogonia of the isolates were quite uniform in size and appearance, varying from 27.5μ to 46.4μ and averaging 38.2μ in diameter. The oospores were spherical, thick-walled, smooth, yellow to amber, 19.9μ to 38.9μ, averaging 30.7μ in diameter. The oogonia and oospores were significantly larger than those obtained by one of the writers (*11*) under higher temperature conditions. Leonian (*5*) describes oospores 25μ to 35μ in diameter; Curzi (*2*) reported oospores 28μ to 35μ in diameter including the persistent oogonial wall, which was at first hyaline but quickly became amber to dark yellow. The antheridia were amphigynous and persistent on the oogonial stalk (fig. 3, *E–G*).

The Honeydew melon isolates agree fairly well with the descriptions of *Phytophthora capsici* in morphologic characters, except for the one culture of *P. drechsleri*.

TEMPERATURE RELATIONS

One of the writers (*11*) used the temperature relations of the species as an aid in distinguishing it. Observations were made on the growth of the 13 isolates on Difco corn-meal agar plates, in triplicate, in controlled temperature chambers at intervals of 5° from 15° to 35° C. (table 1).

TABLE 1.—*Mycelial growth of Phytophthora capsici on Difco corn-meal agar* [1] *plates at different temperatures*

Isolate no.	Average diameter of growth after 96 hours at—					Isolate no.	Average diameter of growth after 96 hours at—				
	15° C.	20° C.	25° C.	30° C.	35° C.		15° C.	20° C.	25° C.	30° C.	35° C.
	Millimeter	*Millimeter*	*Millimeter*	*Millimeter*	*Millimeter*		*Millimeter*	*Millimeter*	*Millimeter*	*Millimeter*	*Millimeter*
1	28	31	58	51	26	8	23	38	55	49	11
2	25	35	58	56	35	9	27	35	56	50	11
3	28	43	64	54	15	10	28	39	54	51	24
4	28	36	64	56	30	11	30	35	58	50	29
5	26	33	56	53	15	12	24	31	54	50	23
6	23	35	50	55	10	13	24	30	55	44	16
7	28	39	59	55	31						

[1] The pH was 6.1.

The optimum temperature probably is slightly under 30° C.; there was usually but little difference in the growth at 25° and 30°, with 12 isolates making more growth at the former. All isolates made some growth at 35°, but there was considerable difference in the amounts. The Honeydew melon isolates exhibited temperature relations typical of *Phytophthora capsici*.

DISTRIBUTION

Although this is the first definite record of the occurrence of *Phytophthora capsici* on a curcurbit, there are a few records of phytophthora infections in which there is a possibility that the species was involved. Drechsler (*3*) in 1926 isolated a species with prominently papillate sporangia from a Honeydew melon from Colorado or California. In 1929 the occurrence of *P. citrophthora* on watermelon, squash, and pumpkin fruits was reported in California (*8*). There are similarities between *P. capsici* and *P. citrophthora*, and it is possible that the species involved was the former.

PATHOGENICITY

A pure culture of *Phytophthora capsici*, isolated from a ripe, partially decayed Honeydew melon, was used in all infection experiments. The fungus was grown on malt-extract agar in Petri dishes, incubated at room temperature, and used for inoculum when 4 days old. Healthy immature, and mature Honeydew melons, selected from a field where the disease was absent, were washed in running tap water, rinsed in distilled water, and dried. A small square of inoculum was placed on the uninjured epidermis and kept moist with absorbent cotton under an inverted preparation dish. No fruits were wounded in any of the inoculation tests. For controls, fruits were handled in the same manner except that sterile agar was substituted for the inoculum.

Six mature Honeydew melons were inoculated, and within 6 days four fruits were infected. The water-soaked, slightly sunken lesions averaged 5 cm in diameter. These artificially induced lesions were identical in color and consistency with those resulting from natural infection. The two noninoculated control fruits remained healthy. The fungus was reisolated from each infected fruit, and three mature melons were inoculated with the reisolated fungus. After 4 days, the lesions on the three infected fruits averaged 7 cm in diameter. The noninoculated controls continued healthy.

Similarly, 12 immature Honeydew melons were inoculated, with 4 melons for controls. After 4 days, seven melons showed typical lesions which averaged 6 cm in diameter. The noninoculated, control melons were healthy. Subsequently, reisolations from infected fruits and inoculations with the reisolated fungus were successful and yielded comparable results.

The approximate daily increase in size of some of the artificially induced lesions was determined by marking their circumferences with an indelible pencil. Lesions of both immature and mature fruits increased in diameter at the rate of more than 2 cm per day.

The results of the inoculation tests indicate that *Phytophthora capsici* is an aggressive parasite, capable of penetrating the uninjured epidermis of either immature or mature Honeydew melons, and that it is the cause of the fruit rot herein discussed.

Inoculations of mature Honeydew melons with *Phytophthora drechsleri* caused water-soaked lesions which differed from those

induced by *P. capsici* in their firmer texture and nonsunken character. Lesions caused by *P. drechsleri* did not tend to split when the fruit was handled, as did the soft, sunken lesions caused by *P. capsici*. *P. drechsleri* spread through the tissues much less rapidly than *P. capsici*.

TESTS FOR SEED TRANSMISSION

Under aseptic conditions, 16 seeds were removed from each of three naturally infected Honeydew melons and planted on poured plates of malt-extract agar. Of the 48 seeds, 18 yielded colonies of *Phytophthora capsici*. While this indicates that the fungus is found on some of the seed coats, it is questionable whether it can survive after the seeds have been removed from the fruit and dried.

Seeds were removed from three naturally infected Honeydew melons and dried at room temperature. Later, 200 seeds from each melon were planted in 6-inch pots of autoclaved soil in a high-temperature greenhouse. Before, during, and after seedling emergence there was no damping-off. The number of seeds which germinated were: Fruit no. 1, 169; fruit no. 2, 157; and fruit No. 3, 155. All pots were watered heavily each day in order to favor possible infection, but none of the seedlings became diseased.

Seeds from a healthy Honeydew melon were planted in pots of autoclaved soil. When the seedlings were 4 inches high, a pure culture of *Phytophthora capsici* on sterilized cracked wheat was added to the soil without injuring the roots. Sterilized cracked wheat was used for the controls. All inoculated and control plants were healthy after 3 weeks. It is of interest to note in this connection that the fungus was not cultured from roots or stems of field-grown plants on which diseased melons were found. These facts suggest that the plant itself is not subject to infection.

Seeds from the three infected and one healthy fruit, previously mentioned, were stored in paper bags at room temperature for approximately 4 months, following which 36 seeds from each fruit were planted on agar plates. *Phytophthora capsici* was not recovered in culture.

Further attempts to isolate the fungus were made by placing 48 seeds from infected fruits and 16 from the normal fruit in slits in mature apple fruits, a method that has proved valuable in isolating some species of *Phytophthora* when other fungi or bacteria are present (*11*). *P. capsici* was not obtained. In every case in which a fungus invaded the apple tissue from the seeds it proved to be a species of *Penicillium* or *Rhizopus*.

As a final test, 25 seeds from each of the 3 infected fruits and 25 seeds from the normal fruit were placed in a germinator at 26° C. After 1 week the seeds from infected fruits showed the following percentages of normal germination: No. 1, 60 percent; no. 2, 24 percent; no. 3, 24 percent. The seeds from the normal fruit produced 80 percent normal seedlings. When seeds from infected fruits that failed to germinate were cultured, *Penicillium* sp. and *Rhizopus* sp. were obtained. Microscopic examination of the seeds failed to reveal sporangia of *Phytophthora capsici*.

The evidence indicates that *Phytophthora capsici* is not transmitted in the seed. Like some other species of *Phytophthora*, the fungus probably lives in the soil as a saprophyte, becoming parasitic only when favorable environmental conditions, such as excess soil moisture and high temperatures, obtain.

EXPERIMENTAL HOST RANGE

In testing other fruits, roots, stems, and tubers for susceptibility to infection by *Phytophthora capsici*, the inoculation technique previously described was used. A suitable number of noninoculated controls was reserved for each species tested. They continued healthy for the duration of the experiments, which were conducted at room temperature (20° to 23° C.). Reisolations were made from all diseased specimens. The reisolated fungus from a particular host was then tested by inoculation into healthy specimens of that host. After infection occurred, isolations were made and the organism was recovered in pure culture.

The host range of the isolate of *Phytophthora capsici* from Honeydew melon, as determined by artificial inoculations in the laboratory, includes 14 species in 11 genera belonging to 6 families, and is as follows:

Lauraceae:
Persea gratissima Gaertn. (avocado).
Rosaceae:
Prunus persica Sieb. and Zucc. (peach—var. Elberta).
Pyrus malus L. (apple—var. Delicious, Jonathan, Esopus Spitzenberg).
Umbelliferae:
Daucus carota L. var. *sativa* DC. (carrot).
Ebenaceae:
Diospyros kaki L. (persimmon).
Solanaceae:
Solanum melongena L. var. *esculentum* Nees (eggplant).
S. muricatum Ait. (pepino).
Lycopersicum esculentum Mill. var. *vulgare* Bailey (tomato—var. Early Santa Clara Canner).
Capsicum annuum L. var. *grossum* Sendt. (bell or green sweet pepper).
Cucurbitaceae:
Cucurbita maxima Duchesne (squash—var. Banana).
C. pepo L. var. *condensa* Bailey (pumpkin—var. Early White Bush Scallop, Pie, Yellow Crookneck, Zucchine).
Citrullus vulgaris Schrad. (watermelon—var. Klondyke).
Cucumis melo L. (muskmelon—var. Dark Green Honeyball, Melo Dew, U. S. No. 45).
C. melo L. var. *inodorus* Naud. (casaba).
C. melo L. var. *reticulatus* Naud. (Persian melon).
C. sativus L. (cucumber).

Infection occurred within a range of 3 to 6 days, depending upon the host involved. In general, decay of tissues was rapid, with slight to marked sinking of the affected areas. Some fruits were completely rotted within a few days. Water-soaked lesions were produced on all hosts except avocado (Hay's maroon),[4] Elberta peach (Saccardo's olive), Delicious and Esopus Spitzenberg apples (chestnut-brown and tawny-olive), eggplant (warm sepia), Yellow Crookneck pumpkin (onion-skin pink), Klondyke watermelon (army brown), and casaba melon (dark olive-buff). Internally, infected tissues of all hosts also were water-soaked in appearance except avocado, apple, eggplant, and watermelon fruits, which showed discolorations comparable to those produced by their surface lesions.

Any fruits, roots, stems, or tubers which failed to become infected at the end of 3 weeks after inoculation were considered to be resistant. Negative results, covering a range of nine families, were obtained: *Ananas sativus* Schult. (pineapple), *Beta vulgaris* L. var. *crassa* Alef. (garden beet), *Brassica campestris* L. var. *napo-brassica* DC. (ruta-

[4] Color determinations were made with the aid of Ridgway's (9) manual.

baga), *B. rapa* L. (turnip), *Pyrus communis* L. (pear—var. Bartlett), *P. malus* L. (apple—var. Bellflower and Yellow Newtown), *Citrus aurantifolia* Swingle (lime), *C. limonia* Osbeck (lemon), *C. grandis* Osbeck (grapefruit), *C. sinensis* Osbeck (orange—var. Valencia), *Pastinaca sativa* L. (parsnip), *Ipomoea batatas* Poir. (sweetpotato), *Solanum tuberosum* L. (potato—var. Russet Burbank), *Cucurbita pepo* L. (pumpkin—var. Cream or Spring and Danish), *C. pepo.* L. var. *ovifera* Bailey (gourds), and *Sechium edule* Swartz (chayote).

In a comparative study of the species of *Phytophthora* one of the writers (*11*) obtained infection and killing of pepper stems inoculated near the tip with cultures of *Phytophthora capsici.* Inoculations with

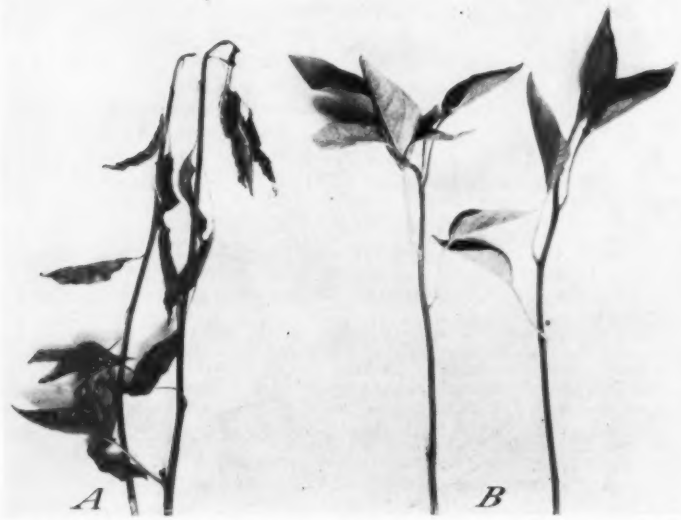

FIGURE 4.—California Wonder pepper plants 10 days after inoculation near the tips: *A*, Inoculated with *Phytophthora capsici* isolated from a Honeydew melon; *B*, inoculated with *Phytophthora parasitica* isolated from a tomato stem.

cultures of other species gave negative results; the pathogenicity of *P. capsici* to pepper stems was, therefore, regarded as a useful criterion for its identification. Pepper plants (California Wonder) 8 to 12 inches tall, were inoculated by placing a bit of mycelium from 2-week-old oatmeal-agar cultures in a small slit near the tip of each stem. Five plants were inoculated with each of two cultures from Honeydew melons identified as *P. capsici.* Both isolates proved virulently pathogenic; after 10 days the terminal portions of the plants were dead and the fungus had invaded and killed the stems to a distance of 3 to 6 inches below the point of inoculation (fig. 4). The results of the inoculations supply confirmatory evidence of the identity of the Honeydew melon fungus.

Parallel inoculations with cultures of *Phytophthora parasitica* isolated from tomato and rhubarb, and with a culture of *P. drechsleri* isolated from a Honeydew melon gave negative results (fig. 4).

Green pepper fruits were inoculated with *Phytophthora capsici* and other species by placing a small tuft of mycelium in a small slit which did not extend into the seed cavity. The wounds were covered with petrolatum and the fruits were incubated in moist chambers at 25° C. The following isolations were used: *P. capsici* (four from Honeydew melons and two from peppers); *P. drechsleri* (one from Honeydew melon); *P. parasitica* (one from *Robinia pseudoacacia* L. and one from *Rheum rhaponticum* L.); *P. citrophthora* (two from *Citrus* in Louisiana and Florida). After 3 days, short tufts of white mycelium appeared in an area about 1 inch in diameter surrounding the wounds in fruits inoculated with *P. capsici;* there was no browning of the tissue; all isolations of this species caused similar symptoms. *P. drechsleri*, *P. parasitica*, and *P. citrophthora* caused a brown discoloration of the fruit tissue in a small area surrounding the wounds, and there was no development of aerial hyphae. After 7 days the fruits inoculated with *P. capsici* were nearly covered with a dense, short, velvety growth of mycelium with some sporangiophores and sporangia. Invasion by the fungus was followed by a bacterial soft rot and the fruits were collapsing; there was no browning of the invaded tissue, but a fading of the normal dark green to a lighter green in the invaded areas. Fruits inoculated with *P. drechsleri*, *P. parasitica*, and *P. citrophthora* showed brown, firm areas nearly 1 inch in diameter at the wounds; there was no aerial mycelium and no soft rot and collapse of the tissues. The inoculations of pepper fruits supplied further evidence that *P. capsici* exhibits certain characteristic pathogenic properties that are uniform in cultures from different hosts and of some value in distinguishing this from other species.

Ten California Wonder and 20 Barbanera no. 1 bell pepper plants were inoculated by mixing 11-day-old cultures of *Phytophthora capsici* from a Honeydew melon with the soil in which they were growing. After 10 days more than half the plants were wilted; after 20 days all California Wonder plants and 19 of the 20 Barbanera no. 1 bell pepper plants were badly wilted and dying.

DISCUSSION

Although the occurrence of phytophthora rot, as shown by surveys of the melon-producing areas of the San Joaquin Valley, was limited to Honeydew melon, it seems probable that this disease might cause damage to other melon crops, such as watermelon, casaba, cantaloup, and Persian, not to mention the many different varieties of squash and pumpkin, if environmental conditions were favorable for the propagation of the fungus and for infection. Careful irrigation and well-drained soil are essential if the disease is to be avoided.

SUMMARY

A rot of honeydew melons was found in part of a commercial planting near Modesto, Calif. The soil had become water-logged owing to lack of proper drainage.

The disease affects both immature (green) and mature (ripe) fruits, but not the vines.

Symptoms of the disease consist of small, incipient brown or water-soaked spots which enlarge to form predominantly large, water-soaked

lesions. Occasionally infected fruits show zonate lesions. Internally, the invaded tissues are soft, water-soaked, and odorless.

The causal organism has been identified as *Phytophthora capsici* Leonian.

Infection of Honeydew melons was obtained by placing inoculum on the unbroken surfaces of the fruit and covering with moist absorbent cotton under an inverted preparation dish.

The incubation period varied from 4 days for immature fruits to 6 days for mature fruits.

Infection of Honeydew melons by *Phytophthora drechsleri* was also demonstrated. However, the fungus spread less rapidly through the tissues which remained firm.

Excessive irrigation, poor drainage, and high temperatures were found to be the chief predisposing factors to infection.

Negative results were obtained in tests for transmission of the fungus in the seed.

In addition to Honeydew melon, the fungus was shown to be pathogenic to 14 species in 11 genera belonging to 6 families.

Avoidance of the disease involves good soil drainage and careful irrigation practice.

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THE INFLUENCE OF COLONY POPULATIONS ON HONEY PRODUCTION[1]

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INTRODUCTION

Two ultimate objectives form the basis of the beekeeper's business, namely, the production of a crop and the conversion of that crop into money. The amount of honey produced per colony has an even greater significance in determining profits than the market price received for the honey.[3] [4]

Many factors affect the yield of colonies and yet very few usable data have been collected upon which an accurate analysis of the significance of any one factor can be based. The intensity and length of the honey flows are of first importance in characterizing differences between seasons, localities, regions, etc. Populations, races or strains of bees, and management contribute to individual variations between colonies and apiaries under the same honey flow. Individual colonies often produce yields many times the average for an apiary. In a broad sense, variations in yield due to differences in population and management are greater under present conditions than those due to the nature of the honey flow. The average beekeeper is not obtaining the maximum production per colony for any particular season or locality.

The purpose of this paper is to outline a method for making an analysis of the influence of colony populations on production, and to give the preliminary results of studies of this relationship carried on by the Intermountain States Bee Culture Field Laboratory.[5]

METHOD OF OBTAINING DATA

Data were collected on the seasonal changes in colony characteristics of colonies individually isolated to prevent drifting. Records of population and production obtained generally at 12-day intervals were used in this analysis. The populations were determined by obtaining the gross weight of the colony and subtracting the weight of the equipment after the bees had been removed. The bees became thoroughly mixed during the manipulation and a sample of 500 to 800 bees was taken from the cluster, weighed, and counted to obtain the average weight per bee in milligrams. This weight was used to convert the total weight of bees into the total number of bees. The usually

[1] Received for publication Jan. 4, 1937; issued July 1937.

[2] Forrest R. Hall, associate professor of commerce, University of Wyoming, has kindly given constructive criticism on the various phases of the statistical procedure employed.

[3] SECHRIST, E. L., and KIFER, R. S. PRELIMINARY REPORT ON APIARY ORGANIZATION AND HONEY PRODUCTION IN THE INTERMOUNTAIN STATES IN 1928. BASED ON STUDIES OF THE BUREAU OF ENTOMOLOGY AND THE BUREAU OF AGRICULTURAL ECONOMICS OF THE UNITED STATES DEPARTMENT OF AGRICULTURE. U. S. Dept. Agr. Rept., 18 pp. 1928. [Mimeographed.]

[4] BURRIER, A. S., TODD, F. E., and SCULLEN, H. A. COST OF PRODUCING HONEY IN OREGON FOR THE YEAR 1931. Oreg. Agr. Expt. Sta., Circ. 83, 13 pp. 1932.

[5] Located at Laramie, Wyo., and maintained cooperatively by the University of Wyoming and the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture.

accepted number of 5,000 bees per pound is unreliable for estimating colony populations since the average for different colonies or for the same colony at different times may range between 2,800 and 4,800 per pound with the majority approximating 3,500. The record of production gives the net increase in honey for the period intervening between the date of the previous observation and that on which the population was determined.

Colony populations tend continuously to change. They either increase or decrease, although normal colonies are capable of maintaining a maximum population of about 60,000 bees during the active season. All normal colonies respond in a similar manner to their environment. It is well known that the intensity of the honey flow varies greatly according to locality, time of season, and weather. Since the required data can be obtained on only a few colonies in one locality at any time (from 6 to 10 per day), it is both desirable and necessary in analyzing the production-population relationship to standardize the production records to a common honey-flow level from which variations induced by locality and time have been eliminated. If this is possible, then production-population data representing a group of colonies taken for any locality, period, or season can be analyzed statistically and readily compared with any other similar data.

DEVELOPMENT OF STATISTICAL METHODS

A graphic comparison of such data in 1932, represented by seasonal segments for 12 colonies individually isolated to prevent drifting and as nearly equivalent in breeding and management as possible, indicated that there is a straight-line relationship between the population of a colony and its production. The production levels for the various seasonal segments differed considerably whereas the slopes of the regression lines indicating the effect of population on production were fairly similar for all segments. Further study of this relationship has resulted in the development of the following statistical method, in some phases unique: The actual production levels of seasonal segments are standardized to a common honey flow of arbitrary intensity for the purpose of determining a significant correlation coefficient and the mean relative production of colonies varying over the normal population range, i. e., 15,000 to 60,000.

The line of regression is determined by the equation

$$Y=r\frac{\sigma_y}{\sigma_x}[X-M_x]+M_y$$

for each seasonal segment of one of more series of colonies. The values of Y (i. e., the production) for the corresponding values of X (e. g., 15,000 and 30,000 bees) for all seasonal segments are averaged to obtain the mean production level for all segments. This mean regression line is all raised (or lowered) proportionally to an arbitrary production level of 15 pounds for 15,000 bees to give the line of standardization. The actual production data for each seasonal segment are standardized by multiplying each by a factor. These factors are obtained by dividing the production indicated on the line of standardization for

the mean population of each seasonal segment by the corresponding actual mean production. The correlation coefficient and regression equation are then computed by the usual methods, using the standardized production data and actual populations for the composite group. When the regression line is determined for the composite standardized data it will fall on the line of standardization (except for negligible differences due to decimals being dropped), giving a check against the computations.

In like manner these standardized regression lines, representing any number of seasons or localities, can be averaged until sufficient data are included to give a better average relationship between colony populations and production. The arbitrary production level of 15 pounds for 15,000 bees used for standardization is entirely within the limits of possible production, although any other level would be equally good in making statistical analyses. It was selected because 15,000 bees is approximately the minimum population for producing colonies. Since the relationship may be better expressed as the "production factor per thousand bees" by dividing any production indicated on the regression line by the corresponding population, the selected standard gives a convenient production factor of unity for producing colonies of minimum population.

APPLICATION OF STATISTICAL METHOD TO DATA

Table 1 summarizes the statistical data obtained from 16 seasonal segments, and the combined standardized data representing a composite of 133 observations, made in 1932 and 1933 on two series of colonies. Table 3 gives the actual population-production data and standardized production data used in determining these constants. The segments are numbered 1 to 16 for the purpose of identifying the actual and standardized regression lines limited by their respective minimum and maximum populations as drawn in figure 1. The high correlation coefficients for most segments indicate a close association between the two factors in question. When the differences in honey flows are eliminated by standardization, the high correlation coefficient of 0.9292 ± 0.0080 is obtained for the composite data. Here the number of cases is sufficiently large to make the coefficient reasonably significant.

Table 2 gives the production factors per thousand bees based on the regression equations given in table 1, the lines of which are drawn in figure 1. When these production factors are averaged for all 16 segments, they may be standardized by dividing each by the average factor for 15,000 bees, to reduce that factor to unity. It will be seen that when these average production factors are standardized, they are equivalent to the production factors obtained from the regression line of the composite standardized data. This duplication of results gives proof that the method presented for standardizing actual productions to a common honey flow does not distort the relationship between the two factors and that the correlation coefficient (r) of 0.9292 ± 0.0080 obtained from the standardized composite data is really significant.

TABLE 1.—*Summary of statistical data obtained in 1932 and 1933 from 16 seasonal segments and combined standardized data showing the population relationship for colonies of bees of three series*

Series and segment no.	Date	Colonies in seasonal segment	Average population (X)	Average production (Y)	Standard deviations		Correlation coefficient (r)	Regression equation	Standardized production for average population	Standardization factor
					σ_x	σ_y				
Isolated series for 1932:		*Number*	*1,000 bees*	*Pounds*	*1,000 bees*	*Pounds*			*Pounds*	
1	July 21	12	22.1	14.4	4.818	6.837	0.8403	$1.1925X-11.95$	27.2	1.889
2	July 27	5	24.3	10.3	5.972	4.116	.6129	$.4224X+.04$	31.0	3.010
3	Aug. 8	5	32.7	27.5	6.117	9.330	.9863	$1.5044X-21.69$	45.4	1.651
4	Aug. 20	6	32.4	40.3	6.237	13.019	.9690	$2.0227X-25.24$	44.9	1.114
5	Sept. 1	6	37.2	10.7	7.107	3.850	.7760	$.4204X-4.94$	53.2	4.972
6	Aug. 2	6	31.2	13.6	6.191	4.948	.8429	$.6736X-7.42$	42.9	3.154
7	Aug. 14	6	37.6	54.0	5.237	11.104	.7214	$1.5296X-3.51$	53.9	.998
8	Aug. 26	6	38.5	41.0	4.493	4.540	.7722	$.7803X+11.00$	55.4	1.351
Isolated series for 1933:										
9	July 20–21	12	20.4	22.2	6.271	9.679	.7264	$1.1212X-.67$	24.3	1.095
10	Aug. 1–2	12	28.8	32.8	7.471	12.798	.8995	$1.5408X-11.58$	38.7	1.180
11	Aug. 13–14	12	36.9	53.8	8.134	16.571	.9198	$1.8739X-15.34$	52.7	.980
Pollen series for 1933:										
12	July 10	9	32.9	18.8	10.229	8.021	.7685	$.6026X-1.03$	45.8	2.436
13	July 23	9	40.8	31.9	10.543	9.097	.8680	$.7489X+1.35$	59.4	1.862
14	Aug. 3	9	44.4	47.8	6.463	13.776	.7537	$1.6065X-23.53$	65.6	1.372
15	Aug. 15	9	47.5	54.3	5.734	9.543	.4445	$.7398X+19.16$	70.9	1.506
16	Aug. 29	9	51.9	51.7	7.086	12.614	.7495	$1.3342X-17.54$	78.5	1.518
Total or average		133						$1.1321X-7.1$		1.515
Line of standardization		133						$1.7200X-10.8$		
Production standardized		133	34.6	48.7	11.5474	21.2719	$0.9_2 92\pm.0080$	$1.7121X-10.54$		

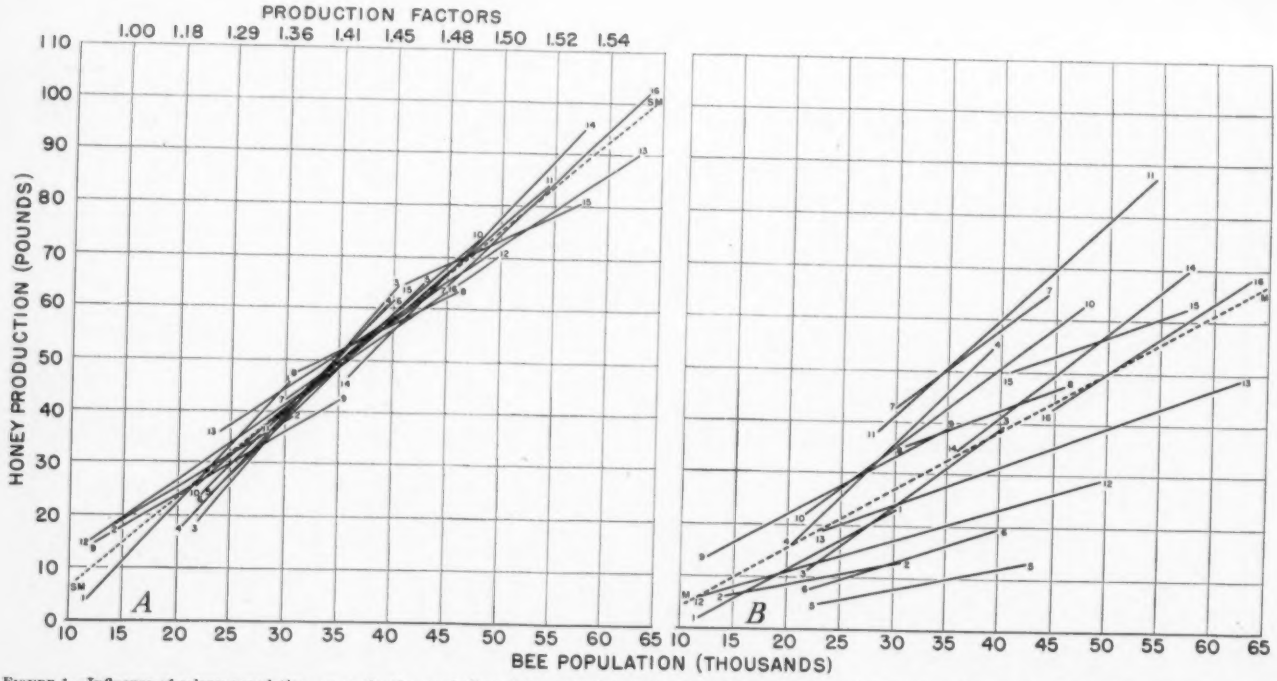

FIGURE 1.—Influence of colony population on production as indicated by statistical data obtained from 16 seasonal segments and two series of colonies, 1932 and 1933: *A*, Standardized mean (*SM*) of seasonal segments—standardized segments (1–16, see tables 1–3) of population ranges; *B*, actual regression lines of seasonal segments (1–16) of population ranges—actual mean (*M*) of seasonal segments.

TABLE 2.—*Production factors per thousand bees based upon seasonal regression lines for actual production and upon standardized regression lines*

Series and segment no.	Date	Production factor per 1,000 bees for colonies of—								
		15,000	20,000	25,000	30,000	35,000	40,000	45,000	50,000	55,000	60,000
Isolated series for 1932:											
1	July 21	0.393	0.595	0.716	0.793	0.851	0.895	0.927	0.954	0.975	0.993
2	July 27	.423	.423	.424	.424	.423	.423	.423	.423	.423	.423
3	Aug. 8	.060	.420	.636	.780	.886	.963	1.022	1.070	1.111	1.143
4	Aug. 20	.340	.760	1.012	1.180	1.303	1.393	1.462	1.518	1.564	1.602
5	Sept. 1	.093	.175	.224	.257	.280	.298	.311	.322	.331	.338
6	Aug. 2	.180	.305	.376	.427	.463	.490	.509	.526	.538	.550
7	Aug. 14	1.293	1.355	1.388	1.413	1.429	1.443	1.451	1.460	1.465	1.472
8	Aug. 26	1.513	1.330	1.220	1.147	1.094	1.055	1.024	1.000	.980	.963
Isolated series for 1933:											
9	July 20–21	1.080	1.090	1.096	1.100	1.103	1.105	1.107	1.108	1.109	1.110
10	Aug. 1–2	.767	.960	1.076	1.153	1.209	1.253	1.284	1.310	1.331	1.348
11	Aug. 13–14	.853	1.105	1.260	1.363	1.434	1.490	1.533	1.568	1.595	1.618
Pollen series for 1933:											
12	July 10	.533	.550	.560	.567	.574	.578	.580	.582	.584	.585
13	July 23	.840	.815	.804	.793	.789	.783	.780	.776	.773	.772
14	Aug. 3	.040	.430	.664	.823	.934	1.013	1.084	1.136	1.178	1.215
15	Aug. 15	2.020	1.700	1.508	1.380	1.289	1.220	1.167	1.124	1.087	1.058
16	Aug. 29	.167	.455	.632	.750	.834	.895	.944	.985	1.015	1.042
Average		.6622	.7793	.8498	.8968	.9309	.9561	.9755	.9914	1.0037	1.0145
Average standardized		1.00	1.18	1.28	1.35	1.41	1.44	1.47	1.50	1.52	1.53
Line of standardization		1.00	1.18	1.29	1.36	1.41	1.45	1.48	1.50	1.52	1.54

The validity of including segment 2 in the composite analysis might be questioned, since this segment covers a production period of only 6 days and all other segments represent practically 12-day periods (table 3). It should be recognized that the production period has no significance in determining the relative production between colonies so long as it is constant for the group. The available nectar varies from day to day, being determined by climatic and honey-plant conditions. Actual gains in honey may be made during only a small portion of the production period whether this covers 6, 10, 12, or even more days. The production periods in this type of analysis, however, should not be too long, since smaller colonies make larger proportional gains in population owing to more intensive brood rearing, [6] permitting these to raise their population-production level within the production period.

TABLE 3.—*Population-production data for colonies of bees in 16 seasonal segments, involving the isolated series for 1932 and the isolated and the pollen series for 1933*

ISOLATED SERIES FOR 1932

Segment and colony no.	Population	Production	Standardization factor	Standardized production
Segment 1 (July 21):	*Thousands*	*Pounds*		*Pounds*
1	21.0	12.1	1.889	22.9
2	24.4	11.6		21.9
3	11.6	3.7		7.0
4	18.1	11.4		21.5
5	21.2	17.7		33.4
6	25.4	21.9		41.4
7	22.4	14.4		27.2
8	16.5	5.9		11.1
9	27.9	15.2		28.7
10	23.3	15.0		28.3
11	22.7	13.1		24.7
12	30.3	31.2		58.9

[6] FARRAR, C. L. THE INFLUENCE OF THE COLONY'S STRENGTH ON BROOD REARING. Ontario Dept. Agr., Beekeepers' Assoc. Ann. Rept. 51–52: 126–130, illus. 1932.

TABLE 3.—*Population-production data for colonies of bees in 16 seasonal segments, involving the isolated series for 1932 and the isolated and the pollen series for 1933*—Continued

ISOLATED SERIES FOR 1932—Continued

Segment and colony no.	Population	Production	Standardization factor	Standardized production
	Thousands	*Pounds*		*Pounds*
Segment 2 (July 27):				
1	24.3	11.0	3.010	33.1
3	14.1	3.3		9.9
4	22.5	15.0		45.2
5	29.9	8.8		26.5
6	30.6	13.6		40.9
Segment 3 (Aug. 8):				
1	33.7	30.5	1.651	50.4
3	21.9	10.9		18.0
4	31.8	24.5		40.4
5	36.0	34.4		56.8
6	40.3	37.2		61.4
Segment 4 (Aug. 20):				
1	36.9	51.5	1.114	57.4
2	20.4	17.3		19.3
3	28.7	28.0		31.2
4	34.6	49.4		55.0
5	34.5	44.8		49.9
6	39.2	50.7		56.5
Segment 5 (Sept. 1):				
1	41.9	13.3	4.972	66.1
2	23.0	5.4		26.8
3	33.5	9.3		46.2
4	39.7	6.5		32.3
5	42.6	14.7		73.1
6	42.7	15.0		74.6
Segment 6, (Aug. 2):				
7	30.9	13.9	3.154	43.8
8	22.1	8.1		25.5
9	38.2	16.7		52.7
10	27.7	14.8		46.7
11	28.3	6.8		21.4
12	40.0	21.3		67.2
Segment 7 (Aug. 14):				
7	44.3	54.5	.998	54.4
8	33.4	36.2		36.1
9	43.4	69.7		69.6
10	35.1	51.8		51.7
11	30.0	46.9		46.8
12	39.7	65.0		64.9
Segment 8 (Aug. 26):				
7	38.4	42.2	1.351	57.0
8	37.0	34.2		46.2
9	46.0	47.1		63.6
10	37.7	39.2		53.0
11	31.0	37.6		50.8
12	40.9	45.9		62.0

ISOLATED SERIES FOR 1933

Segment 9 (July 20–21):				
1	16.3	15.4	1.095	16.9
2	19.6	17.6		19.3
3	18.5	24.4		26.7
4	19.2	32.6		35.7
5	23.4	30.2		33.1
6	16.6	27.0		29.6
7	12.3	14.4		15.8
8	15.5	11.1		12.2
9	31.0	25.8		28.3
10	19.1	13.1		14.3
11	17.9	11.1		12.2
12	35.1	43.5		47.6
Segment 10 (Aug. 1–2):				
1	24.8	31.4	1.180	37.1
2	28.9	25.2		29.7
3	22.2	21.5		25.4
4	27.5	38.6		45.5
5	28.3	28.5		33.6
6	24.8	34.9		41.2
7	23.7	24.0		28.3
8	21.6	14.0		16.5
9	40.7	54.3		64.1
10	29.3	27.1		32.0
11	25.4	33.6		39.6
2	47.8	61.0		72.0

TABLE 3.—*Population-production data for colonies of bees in 16 seasonal segments, involving the isolated series for 1932 and the isolated and the pollen series for 1933*—Continued

ISOLATED SERIES FOR 1933—Continued

Segment and colony no.	Population	Production	Standardization factor	Standardized production
Segment 11 (Aug. 13–14):	*Thousands*	*Pounds*		*Pounds*
1	31.8	41.0	0.980	40.2
2	28.4	45.0		44.1
3	32.0	33.7		33.0
4	38.3	59.1		57.9
5	38.0	55.0		53.9
6	32.6	48.0		47.0
7	33.1	54.5		53.4
8	29.8	34.6		33.9
9	53.4	75.8		74.3
10	36.9	61.9		60.7
11	34.3	43.8		42.9
12	54.4	93.4		91.5

POLLEN SERIES FOR 1933

Segment 12 (July 10):				
2	22.6	19.6	2.436	47.7
3	33.7	22.2		54.1
4	11.9	4.0		9.7
5	37.9	17.6		42.9
6	35.9	17.1		41.7
7	41.1	33.6		81.8
8	49.6	27.4		66.7
9	29.3	15.0		36.5
10	33.8	12.8		31.2
Segment 13 (July 23):				
2	30.6	30.0	1.862	55.9
3	42.9	29.0		54.0
4	23.3	10.5		19.6
5	37.7	32.4		60.3
6	45.8	35.1		65.4
7	48.1	34.4		64.1
8	62.7	47.2		87.9
9	36.7	32.0		59.6
10	39.6	36.8		68.5
Segment 14 (Aug. 3):				
2	38.6	32.6	1.372	44.7
3	48.5	51.8		71.1
4	35.8	21.5		29.5
5	42.2	54.8		75.2
6	46.1	63.6		87.3
7	50.2	66.0		90.6
8	57.6	56.0		76.9
9	41.1	41.0		56.3
10	39.4	42.7		58.6
Segment 15 (Aug. 15):				
2	40.8	51.7	1.306	67.5
3	57.6	72.0		94.0
4	43.4	66.5		86.8
5	46.0	50.4		65.8
6	43.8	56.1		73.3
7	48.9	44.7		58.4
8	57.4	57.7		75.4
9	44.5	49.4		64.5
10	44.8	40.0		52.2
Segment 16 (Aug. 29):				
2	44.8	50.0	1.518	75.9
3	60.5	65.4		99.3
4	63.6	73.9		112.2
5	46.8	50.4		76.5
6	48.4	58.7		89.1
7	60.9	55.2		83.8
8	46.9	31.7		48.1
9	45.6	41.4		62.8
10	49.3	38.3		58.1

APPLICATION OF RESULTS

It will be seen in table 2 that the production per unit of bees substantially increases, on the average, as the population increases. This also holds true in 12 out of 16 segments. Segment 2 did not vary over the population range of 14,100 to 30,600; segments 8, 13, and 15 show decreases in production per unit of bees although all three represented comparatively narrow population ranges. The standardized production factors per unit of bees may be interpreted to mean that one colony with 60,000 bees will probably produce 1.54 times as much honey as four colonies each with 15,000 bees; one colony with 45,000 bees will probably produce 1.48 times as much honey as three colonies each with 15,000 bees; one colony with 30,000 bees will probably produce 1.36 times as much honey as two colonies each with 15,000 bees.

In localities where the honey flow is of short duration, ranging from 10 to 40 days, the significance of this marked advantage in strong colonies is readily apparent. In localities having an extended honey flow lasting from 60 to 90 days, as is characteristic of the intermountain region, the advantage of strong colonies at the beginning of the flow is still evident although to a less extent than where the flow is short. This situation results from the fact that smaller colonies rear more brood in proportion to their population than do large colonies [7] and are thus able to gain in strength more rapidly. The stronger colony actually rears more brood, other things being equal, than do smaller colonies and is thus able to maintain its advantage until a maximum strength of approximately 60,000 bees is reached for all colonies.

The same amount of honey can be produced from a small number of strong colonies at a greater saving in both labor and equipment than from a larger number of small colonies. This fact is particularly significant in determining profit or loss under low honey prices and it should be recognized as a sound business principle when dealing with a favorable market.

SUMMARY AND CONCLUSIONS

A high correlation and a linear relationship were found to exist between the populations of small groups of colonies and their respective productions during periods of less than 2 weeks when all colonies had access to the same source of nectar for the same period of time. The production level varied between seasonal or locality segmental groups of colonies owing to differences in the amount of nectar available, but the relative production slopes of 16 segments when reduced to standard production factors per unit of bees were found to be fairly similar.

A method was developed of standardizing segmental population-production data to a standard honey-flow level by averaging the actual regression lines of the segmental data. This average line is raised (or lowered), all points proportionally, to a selected standard where 15,000 bees produce 15 pounds of honey. A standardization factor is obtained for each segment by dividing the production indicated on the line of standardization for its mean population by its respective actual mean production. The actual production for each

[7] FARRAR, C. L. See footnote 6.

colony in a segment is then multiplied by the standardization factor representative of its segment to obtain the standardized production. When the standardized production for each of 133 cases representing 16 seasonal segments was correlated with the actual population, a correlation coefficient of 0.9292 ± 0.008 was obtained. The resulting regression equation was determined and found practically to coincide with the line of standardization. When this line was reduced to factors representing the mean relative production per thousand bees over the normal colony population range it was found that bees in colonies with 30,000, 45,000, and 60,000 bees produced at a rate of 1.36, 1.48, and 1.54 times as much honey, respectively, as colonies with 15,000 bees.

The lines representing the slopes of the different seasonal segments and extending over the normal population range, i. e., 15,000 to 60,000 bees, were factored. These factors when averaged and reduced to the standard of unity of 15,000 bees, were the same as those derived from the regression line of the composite standardized data. This procedure demonstrates that the standardization method does not distort the relationship existing between the actual population and production data and indicates that the coefficient of correlation, 0.9292, thus obtained can be considered significant.

The conclusion may be drawn from the production factors derived that the production efficiency of colonies increases as the population increases throughout the normal population range of 15,000 to 60,000 bees.

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